

ACTIVITY PATTERNS AND HABITAT ASSOCIATIONS
OF KEMP'S RIDLEY TURTLES, *Lepidochelys kemp*,
IN THE COASTAL WATERS OF THE CEDAR KEYS, FLORIDA

By

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By

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Radio and sonic telemetry were used to investigate the site fidelity, tidal orientation, rate of movement (ROM), respiratory behavior, and habitat associations of Kemp's ridley turtles, *Lepidochelys kemp*. Nine turtles were tracked east of the Cedar Keys, Florida, for up to 70 days after release and occupied 5 - 30 km² foraging ranges. The mean of mean turtle bearings on incoming ($48 \pm 49^\circ$) and falling ($232 \pm 41^\circ$) tides were significantly oriented to the mean directions of tidal flow ($37 \pm 9^\circ$, $p < 0.0025$, and $234 \pm 9^\circ$, $p < 0.005$, respectively). Turtles had a mean ROM of 0.44 ± 0.33 km/hr (range: 0.004 - 1.758 km/hr), a mean surface duration of 18 ± 15 seconds (range: 1 - 88 seconds), and a mean submergence duration of 8.4 ± 6.4 minutes (range: 0.2 - 60.0 minutes). ROM was negatively correlated with surface and submergence durations and

positively correlated with the number of surfacings. Furthermore, ROMs were higher and surface and submergence durations were shorter during the day.

Habitat associations of Kemp's ridley turtles were analyzed in terms of availability, utilization, and preference using compositional analyses. Forty-eight percent of the study area consisted of sand bottom, but over half of the sand sites had rock outcroppings. Seagrasses comprised 16% of the available habitat, green macroalgae comprised 12%, live bottom and red macroalgae each comprised 7%, and the Corrigan Reef oyster bars comprised < 2%. Six of the turtles utilized unvegetated sand and rock bottom surrounding Corrigan Reef (65 - 78% of foraging ranges and 64 - 82% of locations), and three turtles utilized the vegetated southern region (37 - 64% of foraging ranges and 31 - 57% of locations). Compositional analyses indicated that turtles used rock outcroppings in their foraging ranges at a significantly higher proportion than available within the study area. Additionally, live bottom and green macroalgae were utilized significantly more than seagrasses. Water depth ranged from intertidal oyster reefs to depths > 3 m, but turtles preferred 1-3 m depths within their foraging ranges. Daily activities of turtles were attributed to food acquisition and bioenergetics, while their habitat associations may be correlated to habitat structure, prey availability, competition, and developmental stage.

CHAPTER 1 KEMP'S RIDLEY TURTLE CONSERVATION AND RESEARCH

Conservation History

The Kemp's ridley turtle, *Lepidochelys kemp*i, is the most endangered species of marine turtle ([Ross et al., 1989](#); [Magnuson et al., 1990](#)). Human impacts on the various life history stages of the Kemp's ridley turtle have resulted in their rapid decline in numbers. Exploitation of eggs ([Hildebrand, 1982](#)), slaughter of nesting females ([Pritchard, 1969](#)), commercial fisheries for subadults and adults ([Pritchard and Márquez, 1973](#); [Márquez, 1994](#)), and incidental capture of subadults and adults in shrimp trawls ([Ross et al., 1989](#); [Magnuson et al., 1990](#)) have been identified as causes for the population decline. Initial efforts to conserve this species concentrated on protecting the primary rookery at Rancho Nuevo, Tamaulipas, Mexico, where almost the entire population of adult female Kemp's ridley turtles come ashore to nest ([Márquez, 1994](#)). During recent years, efforts have focused on reducing the capture of Kemp's ridley turtles in the U.S. and Mexican shrimp fisheries.

Prior to 1961, the location of Kemp's ridley rookeries was unknown until a documentary film made in 1947 was discovered by marine turtle biologists ([Carr, 1963](#); [Hildebrand, 1963](#)). In this film, an estimated 40,000 females nested during the daylight hours in a single nesting aggregation known as an arribada (Spanish

for “arrival”). By 1966, when the Mexican government established the first protection camp at Rancho Nuevo, these arribadas only reached 2,000 turtles ([Márquez, 1994](#)). This rapid decrease in numbers was attributed to decades of heavy human exploitation of adult females and their eggs, coupled with the natural predation at the nesting beach, which resulted in virtually no recruitment to the aging adult population. Protection of the nesting beach by Mexican authorities essentially halted the exploitation of the females and their nests. The U.S. government listed the Kemp’s ridley turtle as endangered in 1970 and federal protection of the species was initiated under the Endangered Species Act of 1973 and subsequent amendments ([Magnuson et al., 1990](#)).

Since 1978, Mexican and U.S. authorities have participated in a cooperative program for Kemp’s ridley research and conservation. During each nesting season, biologists from both countries patrol the beaches of Rancho Nuevo, measure and tag nesting females, and relocate eggs to protected corrals. The hatchery program has been closely monitored and has resulted in the release of approximately 20,000 hatchlings annually from 1966-78 and 50,000 thereafter ([Márquez, 1994](#)). The number of nesting females provides the best available index for the size of the Kemp’s ridley population ([Magnuson et al., 1990](#)) and has been calculated from the total number of nests divided by the average number of nests deposited by females each year. This population parameter is particularly sensitive to the annual number of clutches laid by females, and estimates have ranged from 1.5 to 3 nests/female/season ([Rostal et al., 1997](#)). Therefore, the total number of nests observed at Rancho Nuevo

has been the standard used to assess the status of the species ([U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992](#)).

Despite intensive protection of the nesting beach, the reproductive output of the population steadily declined from a total of 954 nests in 1979 to a low of 702 nests in 1985 ([U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992](#)). Incidental capture of subadult and adult turtles in commercial fisheries, particularly shrimp trawling, was identified as the major source of mortality hindering the restoration of the species ([Ross et al., 1989](#); [Magnuson et al., 1990](#)). In 1987, regulations were enacted requiring the seasonal use of turtle excluder devices (TEDs) in shrimp trawlers operating in the offshore waters from North Carolina to Texas. By 1994, legislation was passed requiring year-round use of TEDs in all shrimp trawlers operating in U.S. waters. In addition, the Mexican government announced in 1993 that offshore shrimp trawlers operating in the Gulf of Mexico and Caribbean Sea would be required to use TEDs.

There are indications that the binational conservation efforts of the past three decades may be benefiting the highly endangered Kemp's ridley turtle. The number of nests recorded at Rancho Nuevo has been steadily increasing since the mid-1980's. Newly established camps to the north and south of Rancho Nuevo are also reporting increases in nest numbers ([Márquez et al., 1996](#)). In 1998, researchers recorded 2,409 nests at Rancho Nuevo, which was the highest observed level of nesting in 27 years ([Márquez et al., 1999](#)). Protection of the nesting beach has presumably led to increased numbers of subadult turtles in U.S. coastal waters, but there are no quantitative data to substantiate this

supposition ([Ogren, 1989](#); [Ross et al., 1990](#); [Schmid, 1998](#)). Increased nesting may be attributable to the reduced mortality of adults and subadults resulting from the restrictions placed on the shrimp fishery ([Turtle Expert Working Group, 1998](#); [Márquez et al., 1999](#)). Nevertheless, the status of the Kemp's ridley turtle remains precarious as nesting intensity is still drastically reduced when the baseline is shifted to historical levels ([Fig. 1-1](#)). Furthermore, human encroachment in critical habitats, such as the nesting beach and coastal foraging grounds, continues to threaten the recovery of this species.

Research Efforts

As with the conservation efforts, much of the research conducted on Kemp's ridley turtles has focused on the reproductively active females. Tagging studies have indicated that female Kemp's ridley turtles leave the Mexican nesting beach and migrate northward to feeding grounds offshore of Louisiana or southward off of Campeche ([Pritchard and Márquez, 1973](#)). Satellite telemetry has demonstrated that the females typically travel in continental shelf waters less than 50 m deep ([Byles, 1989](#); [Byles and Plotkin, 1994](#)). Virtually nothing is known about adult male Kemp's ridley turtles other than their occurrence off the nesting beach during mating ([Ross et al., 1990](#)).

A number of authors have proposed dispersal scenarios for hatchling Kemp's ridley turtles once they have left the Rancho Nuevo nesting beach ([Pritchard and Márquez, 1973](#); [Carr, 1980](#); [Collard, 1990](#); [Collard and Ogren, 1990](#)), but there is little information concerning their actual pelagic development.

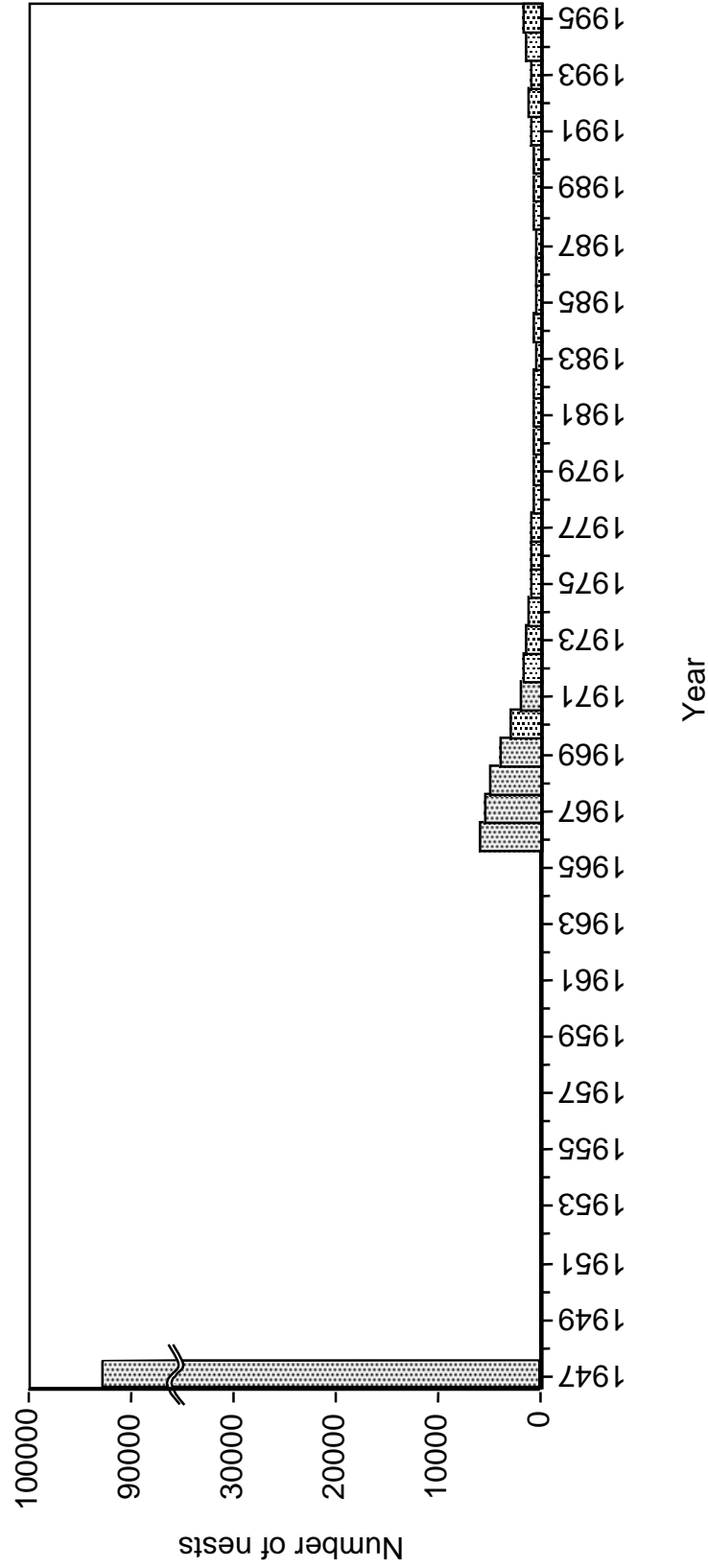


Figure 1-1. Historical records of the annual number of Kemp's ridley turtle nests at Rancho Nuevo, Mexico (estimate for 1947 from [Magnuson et. al, 1990](#); data for 1966-95 from [Turtle Expert Working Group, 1998](#)).

[Collard and Ogren \(1990\)](#) hypothesized that post-hatchling Kemp's ridleys become entrained within the Mexican Current and are then transported to the Loop Current or a Loop Current eddy via an eastward flowing jet in the northwestern Gulf of Mexico ([Fig. 1-2](#)). Wind-driven surface currents west of the Mississippi River or Loop Current eddies to the east may eject turtles into the coastal waters of the northern Gulf. Kemp's ridley turtles embedded within the Loop Current are transported out of the Gulf through the Straits of Florida and then carried northward by the Florida Current/Gulf Stream. Individuals in the western edge of the Florida Current/Gulf Stream may enter the coastal waters of New England either by actively swimming shoreward or by passive transport in meanders or warm-core eddies of the Gulf Stream ([Carr, 1980](#); [Collard and Ogren, 1990](#)). Some turtles remain within the Gulf Stream where they are transported across the North Atlantic Ocean to the coasts of the Azores and Europe ([Pritchard and Márquez, 1973](#); [Carr, 1980](#); [Brongersma, 1982](#); [Bolten and Martins, 1990](#); [Márquez, 1994](#)). There has been considerable debate as to whether these individuals are able to survive in the North Atlantic Gyre and recruit to the Gulf of Mexico breeding population ([Carr, 1980](#); [Ogren, 1989](#); [Collard and Ogren, 1990](#)).

Post-pelagic Kemp's ridley turtles (20 - 25 cm straight-line carapace length [SCL]) recruit to inshore waters from Texas to Massachusetts and begin a coastal-benthic stage of development. The smallest turtles in U.S. waters have been found in New England and this observation supports the hypothesis that pelagic juveniles are transported out of the Gulf of Mexico, travel northward with

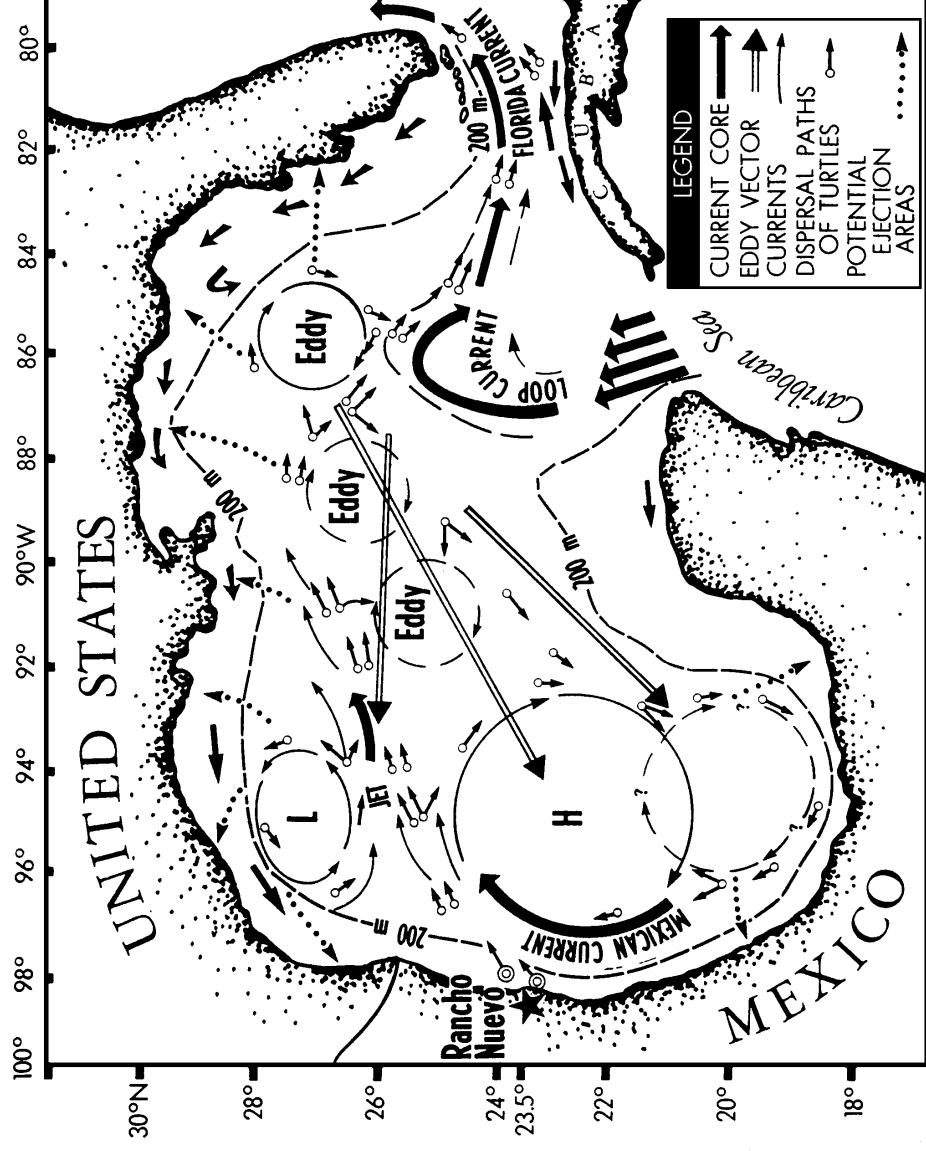


Figure 1-2. Surface circulation and hypothetical dispersal paths of epipelagic Kemp's ridley turtles in the Gulf of Mexico (from [Collard, 1990](#)).

the Florida Current/Gulf Stream, and then shoreward to the northeastern seaboard (Carr, 1980; Ogren, 1989). The smallest post-pelagic turtles in the Gulf of Mexico are found in the coastal waters of the Texas-Louisiana border and the Florida panhandle east of Cape San Blas (Ogren, 1989). Collard and Ogren (1990) suggested that these two areas were ejection points for juvenile turtles that have completed their pelagic development within the Gulf. In-water research methods are necessary to investigate the Kemp's ridley turtles that occur in the estuarine systems along the Atlantic and northern Gulf coasts. The remainder of this chapter will focus on the tagging and telemetric studies that have been used to characterize the aggregations of wild, subadult turtles in U.S. coastal waters.

Tagging Studies

In 1955, Carr and Caldwell (1956) conducted tagging experiments with Kemp's ridley turtles captured in the former turtle fishery of west Florida and provided the first scientific data for this species. Further investigations of Kemp's ridley turtles in U.S. coastal waters were not initiated until after their listing in the Endangered Species Act of 1973. Since then, long-term tagging studies have characterized the size classes, seasonal occurrence, long-distance migrations, local movements, and growth of subadult turtles in the northwestern Atlantic Ocean and the northern Gulf of Mexico.

Size classes

Ogren (1989) described the life history of the Kemp's ridley turtle as a juvenile epipelagic stage (< 20 cm SCL), a coastal-benthic subadult stage (20-60 cm SCL), and a coastal-benthic adult stage (> 60 cm SCL). Carr (1980) and Ogren (1989) suggested an increasing north-south size gradient for subadult turtles along the U.S. Atlantic coast. Smaller turtles are typically captured in New England (\bar{x} = 30 cm SCL in New York waters; Standora et al., 1992), but an increasing gradient in mean size or size class composition is not observed when comparing collections of Kemp's ridley turtles from Virginia, South Carolina/Georgia, and Florida (Fig. 1-3). All the aggregations were primarily composed of early to mid-subadults (20-40 cm SCL) with the exception of a few adult-size turtles captured in east-central Florida. However, these distributions and measures of central tendency are subject to error owing to small sample sizes and sampling bias. The comparison is further complicated by the fact that individuals move among these areas seasonally (see following section).

A clinal size pattern has not been observed for Kemp's ridley turtles in the northern Gulf of Mexico (Ogren, 1989), although there were indications that larger turtles occur in deeper water offshore (Rudloe et al., 1991). A comparison of the mean sizes and size class compositions from northwestern and west-central Florida does suggest an increasing north-south size gradient in the eastern Gulf (Fig. 1-3). Sixty-six percent of the turtles captured in the Florida panhandle were early to mid-subadults (Rudloe et al., 1991), compared to 24% in the Cedar Keys (Schmid, 1998). However, this observation may be the result of

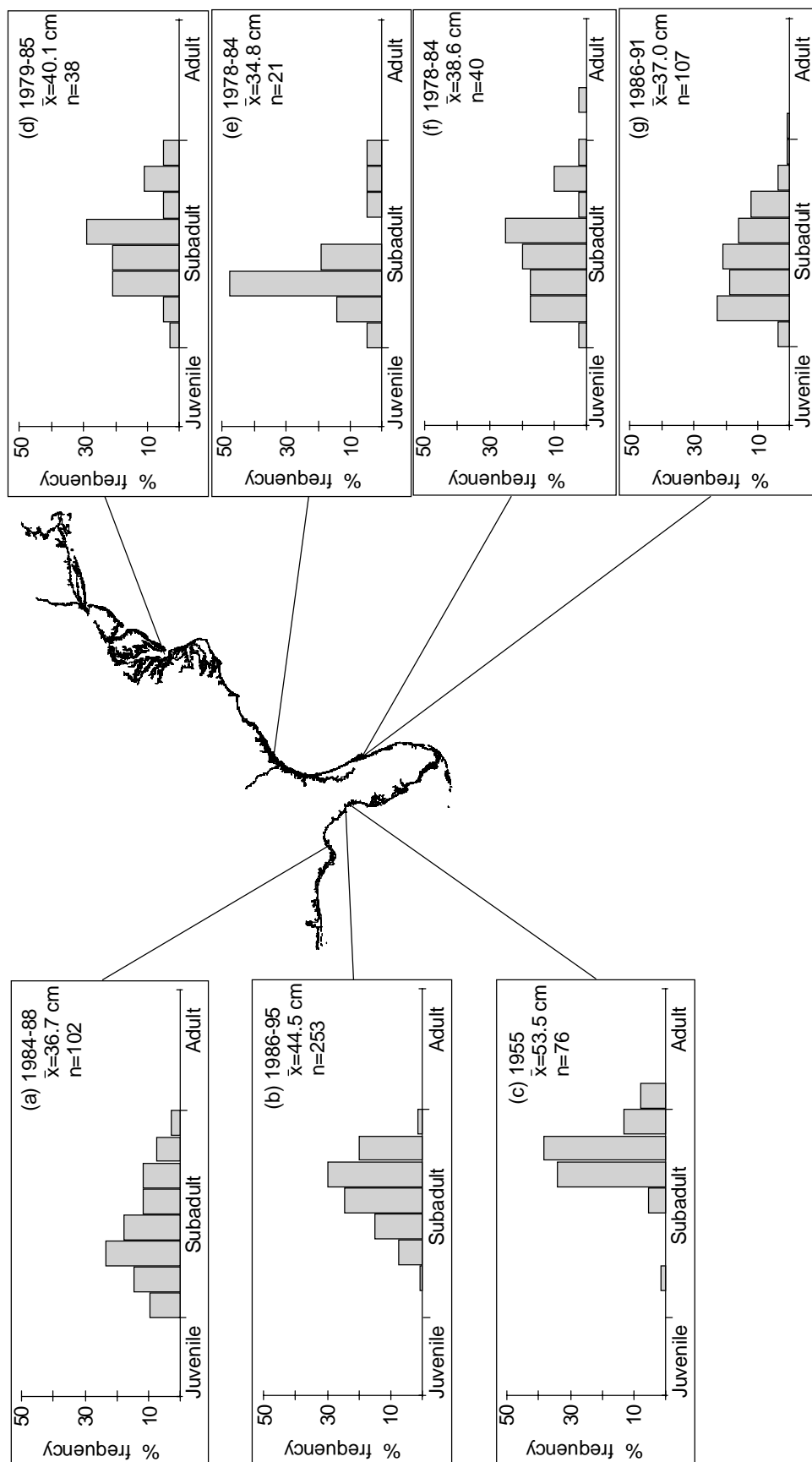


Figure 1-3. Size class compositions for Kemp's ridley turtles in (a) western Apalachee Bay (Rudloe et al., 1991), (b) Cedar Keys (Schmid, 1998), (c) Withlacoochee and Crystal Rivers (Carr and Caldwell, 1956), (d) Chesapeake Bay (Byles, 1988), (e) Georgia/South Carolina waters (Henwood and Ogren, 1987), and (f and g) Cape Canaveral (Henwood and Ogren, 1987 and Schmid, 1995, respectively).

gear bias as the former study was based on turtles captured in commercial fisheries, primarily shrimp trawls, and the latter was based on fishery-independent captures with entanglement nets. Large-mesh tangle nets are known to favor the capture of larger turtles ([Carr and Caldwell, 1956](#); [Schmid and Ogren, 1992](#)).

A temporal difference has been noted in size distributions of Kemp's ridley turtles in west-central Florida ([Schmid, 1998](#)). All but one of the turtles examined by Carr and Caldwell in the mid-1950s were greater than 40 cm and 8% of the specimens were greater than 60 cm SCL ([Fig. 1-3](#)). By comparison, 24% of the turtles captured from 1986 to 1995 were 20-40 cm SCL and 76% were 40-60 cm SCL. Gear bias was ruled out as both studies utilized large-mesh tangle nets. The observed difference could be indicative of a demographic shift which has resulted from the protection of the nesting beach over the past three decades ([Schmid, 1998](#)). However, Carr and Caldwell relied upon captures from the commercial fishery and larger turtles may have been preferentially landed given their higher market value. Interestingly, some Cedar Keys turtle fishermen referred to smaller turtles as "housekeepers" which were customarily released to "tend the house" of the larger turtles (Schmid, pers. obs.). This anecdote may explain the lack of smaller size classes in the turtle fishery and suggests the fishermen may have been practicing the first conservation efforts for this species.

Seasonal occurrence and migrations

Subadult Kemp's ridley turtles are captured as far north as Cape Cod Bay, and occur in Long Island Sound ([Morreale and Standora, 1998](#)) and Chesapeake

Bay ([Musick and Limpus, 1997](#)) between June and November. Increasing numbers of turtles are captured off Cape Canaveral from January to March ([Henwood and Ogren, 1987](#); [Schmid, 1995](#)). The results of tagging studies along the Atlantic coast indicate a seasonal north-south migration of subadult Kemp's ridley turtles. Turtles tagged off the Florida east coast during the winter have been recaptured in northeastern waters during the summer, and turtles tagged in northeastern waters in summer have been recaptured off Florida in winter ([Henwood and Ogren, 1987](#); [Schmid, 1995](#)). In recent years, Kemp's ridley turtles tagged on the east coast have been observed nesting at Rancho Nuevo ([Schmid, 1995](#); [Schmid and Witzell, 1997](#); [Witzell, 1998](#)), providing support that subadult turtles in the Atlantic recruit to the Gulf of Mexico breeding population.

Kemp's ridley turtles are captured in the nearshore waters of the northeastern Gulf of Mexico from April to November ([Carr and Caldwell, 1956](#); [Schmid and Ogren, 1990, 1992](#); [Schmid, 1998](#)). [Ogren \(1989\)](#) proposed an offshore migration based upon the capture of turtles in deeper waters during the winter ([Rudloe et al., 1991](#)). Tag-recapture data along the northern Gulf coast have demonstrated east-west movements of subadult Kemp's ridley turtles ([Carr, 1980](#); [Ogren, 1989](#)). However, there are no recoveries that indicate a seasonal migration in the eastern Gulf ([Schmid, 1998](#)). Turtles in the northern Gulf may be moving to warmer waters offshore or may travel southward as has been demonstrated for their Atlantic conspecifics.

Local movements

Kemp's ridley turtles have been recaptured at sites of initial capture within a relatively short period, indicating fidelity to specific areas during their seasonal occurrence in coastal waters. [Carr and Caldwell \(1956\)](#) noted that a turtle released in the Cedar Keys traveled approximately 35 km to the original capture site at the Withlacoochee-Crystal River fishing grounds within 43 days. Short-term fidelity to capture sites has also been observed along the eastern seaboard in Long Island Sound ([Morreale and Standora, 1998](#)), Chesapeake Bay ([Musick and Limpus, 1997](#)), and Cape Canaveral ([Schmid, 1995](#)). In addition to short-term recaptures, long-term and multiannual recaptures of Kemp's ridley turtles in the Cedar Keys indicate that turtles remigrate to capture sites and may do so for at least 4 years ([Schmid, 1998](#)).

Growth

Marine turtle studies commonly report growth rates in terms of the annual increase in the carapace length between initial capture and subsequent recapture. Tagging studies of wild, subadult Kemp's ridley turtles have yielded little information on growth owing to the lack of recapture data and the short duration of recaptures that have been recorded. Extrapolating annual growth rates from short-term recaptures will amplify errors associated with the carapace measurements and will yield overestimates during periods of rapid growth. Kemp's ridley turtles recaptured during their seasonal occurrence at the Cedar Keys exhibited a significantly higher growth rate (7.7 ± 3.6 cm/yr) than that for

turtles recaptured between seasons (3.3 ± 1.1 cm/yr; [Schmid, 1998](#)). However, all within-season recaptures were less than 180 days. Recaptures between seasons were of longer duration and the growth rates for these turtles may be more representative of the yearly increase in carapace length.

The removal of short-term recaptures increases the accuracy of annual growth rate estimates ([Table 1-1](#)), but also decreases the sample size. Growth rates of 6 - 9 cm/yr were calculated for Kemp's ridley turtles captured in Cape Canaveral ([Table 1-1](#)). However, all but one of the turtles in this study were recaptured in less than a year. Growth rates of 4 - 5 cm/yr were calculated for turtles collected at the Cedar Keys ([Table 1-1](#)). Approximately half of the recaptures in this latter study were greater than one year duration, thus decreasing extrapolation error. Furthermore, precision was increased as all measurements were performed by a single person using the same equipment ([Bolten, 1999](#)). A comparable growth rate of 4.0 cm/yr was reported from short-term recaptures of Kemp's ridley turtles in New York waters ([Morreale and Standora, 1998](#)).

Growth models have been applied to marine turtle mark-recapture data in order to estimate population parameters such as the age of reproductive maturity and the duration of life history stages. The Kemp's ridley turtle datasets from Florida were fitted with the von Bertalanffy growth equation ([Table 1-1](#)), but the

Table 1-1. Mean annual growth rates and estimated values of asymptotic length and intrinsic growth rate from the von Bertalanffy growth interval equation for Kemp's ridley turtles captured in Florida (standard errors in parentheses).

Data treatment	Mean growth rate (cm/yr)	Sample size	Asymptotic length	Intrinsic growth rate
1) Cape Canaveral database (Schmid, 1995)				
All recaptures	8.3 (2.8)	12	61.1 cm (5.4)	0.5774 (0.2176)
All recaptures > 90 days	8.8 (4.2)	6	60.7 cm (8.0)	0.6037 (0.3549)
All recaptures > 180 days	5.9 (1.0)	3	77.9 cm (21.1)	0.2466 (0.1771)
2) Cedar Key database (Schmid, 1998)				
All recaptures	5.4 (0.7)	24	91.4 cm (41.9)	0.0852 (0.0720)
All recaptures > 90 days	4.5 (0.7)	16	90.9 cm (51.1)	0.0858 (0.0892)
All recaptures > 180 days	3.6 (0.3)	13	77.3 cm (29.2)	0.1167 (0.0957)
3) Combined database (Schmid and Witzell, 1997)				
All recaptures	6.4 (1.0)	36	80.0 cm (30.5)	0.1292 (0.1060)
All recaptures > 90 days	5.6 (1.2)	22	81.40 cm (42.7)	0.1241 (0.1370)
All recaptures > 180 days	4.0 (0.4)	16	178.0 cm (424.0)	0.0343 (0.1072)

resulting asymptotic lengths were either underestimated (Cape Canaveral) or overestimated (Cedar Key) when compared to the mean length of nesting Kemp's ridley turtles (64.2 cm converted SCL; [Schmid and Witzell, 1997](#)). Small sample sizes with truncated distributions of lengths, combined with differences in growth rates within and between these two areas, were identified as factors affecting the growth model parameters. Consequently, the datasets were combined and the growth equation for all recaptures was selected as the best fit ([Table 1-1](#)). This growth equation estimated age to maturity at 8 - 9 years for the smallest nesting female (56.0 cm converted SCL; [Burchfield et al., 1988](#)) and 10 - 11 years for 60 cm SCL adult-size turtles ([Ogren, 1989](#), [Schmid, 1995](#), [1998](#)). In addition, the estimated age of the smallest turtle (26.3 cm SCL, 2.6 years) and largest turtle (61.8 cm SCL; 11.0 years) in the combined dataset suggested an 8 - 9 year duration for the coastal-benthic subadult stage ([Schmid and Witzell, 1997](#)). However, the von Bertalanffy model assumes a steadily decreasing growth rate during the succession of developmental stages and recent evidence suggests ontogenetic variation in the growth rates of Kemp's ridley turtles ([Zug et al., 1997](#)). Consequently, polyphasic growth models have been proposed for this species ([Chaloupka and Zug, 1997](#)).

Telemetry Studies

Recoveries of tagged turtles reveal endpoints and periodicities of migration, but yield little information on activities between capture and recapture ([Carr, 1980](#); [Meylan, 1982](#)). The introduction of radio ([Baldwin et al., 1969](#)),

ultrasonic ([Ireland, 1980](#)), and satellite ([Timko and Kolz, 1982](#)) telemetry techniques to marine turtle studies increased our ability to investigate the free-ranging behavior of turtles and thus fill the data gaps of mark-recapture studies. Radio and sonic transmitters have been applied to subadult Kemp's ridley turtles to investigate their short-term movements and activities, while satellite transmitters have been used to document long-term migrations and activities.

Movements and migrations

The primary goal of the telemetric studies on Kemp's ridley turtles has been to describe their movements and migrations. Subadult turtles tracked via radio and sonic transmitters in Cape Cod Bay ([Danton and Prescott, 1988](#)) and Chesapeake Bay ([Bytes, 1988](#)) frequented shallow-water, seagrass shoals and exhibited strong tenacity to specific areas. [Bytes \(1988\)](#) also noted that Kemp's ridley turtles did not appear to orient their movements with the direction of tidal flow as was observed for loggerheads, *Caretta caretta*. Similar investigations in New York waters have shown that Kemp's ridley turtles may reside near the point of capture for up to 121 days ([Morreale and Standora, 1998](#)). Most of the movements by turtles in this latter region were during the day ([Standora et al., 1989](#)). Furthermore, turtles exhibited nondirected movements indicative of foraging behavior from July to September when water temperatures were $> 15^{\circ}\text{C}$ ([Standora et al., 1990](#); [Morreale and Standora, 1998](#)). More directed movements were observed in September and October when water temperatures were $< 15^{\circ}\text{C}$, and these eastward movements corresponded to departure from

coastal estuaries into the Atlantic Ocean. A southward migration during the fall was indicated by two turtles that left the nearshore waters of Georgia in October and traveled along the coast of northeastern Florida through November ([Gitschlag, 1996](#)).

Satellite telemetry has been used to document the seasonal north-south migration of Kemp's ridley turtles along the Atlantic seaboard. Subadult turtles emigrate from New England waters in October and November and continue their migration southward off the coasts of Virginia and North Carolina through November ([Standora et al., 1992](#); [Morreale and Standora, 1998](#)). Two separate studies have documented overwintering in Florida and remigration northward the following spring. A subadult turtle (< 60 cm SCL; [Renaud, 1995](#)) and an adult-size turtle (60.7 cm; [Gitschlag, 1996](#)) traveled southward from the coastal waters of Georgia and northern Florida in October and November, remained in coastal waters south of Cape Canaveral from December through February, moved northward in March and April, and resided off the South Carolina coast through July. Satellite telemetry has also been used to document a west to east migration in the Gulf of Mexico ([Renaud, 1995](#)). An adult-size turtle (60 cm SCL) held captive for a year was released from south Texas in March, traveled across the northern Gulf through August to waters offshore of west-central Florida, and was last recorded north of Key West in December. The movements of this turtle during the latter portion of the tracking interval indicate a possible southerly migration for Kemp's ridley turtles in the eastern Gulf.

Behavior

Behavioral studies of Kemp's ridley turtles in U.S. coastal waters have focused on patterns of respiratory durations, but it is difficult to compare the results among studies owing to the different telemetric methodologies. The data obtained from satellite transmitters are in terms of submergence patterns and are summarized in 12-hour intervals, whereas the data obtained from radio transmitters are in terms of surfacing patterns and are collected consecutively. Nevertheless, some comparisons can be made between methodologies with respect to submergence duration. Mean submergence durations recorded from radio transmitters were generally less than those recorded via satellite and the durations for backpack attachments were greater than tethered attachments for both types of transmitters ([Table 1-2](#)). [Standora et al. \(1992\)](#) noted that a backpack satellite transmitter would often indicate a turtle was diving when the animal was a few centimeters below the surface and recommended tethered transmitters for recording diving behavior. All telemetric studies have reported relatively high percentages of time submerged for Kemp's ridley turtles except [Morreale and Standora \(1998; Table 1-2\)](#). This latter study was conducted in New England waters, where smaller turtles are known to occur, and the variability in percent time submerged could be related to the transition between developmental stages. New recruits from the pelagic stage may spend more time at the surface than turtles that have already become established in the coastal-benthic habitat.

Table 1-2. Mean surface and submergence durations for non-nesting Kemp's ridley turtles in U.S. coastal waters.
Brackets indicate extrapolated values.

Transmitter/attachment	Life history stage ^a	Sample size	Mean surface duration (sec)	Mean submergence duration (min)	% time submerged
Radio/tether ^b	Subadults	2	126.0	12.7	[83.5]
Radio/backpack ^c	Subadults	2	[90.0]	[27.0]	95
Radio/tether ^d	Subadults	16	-	-	1.7 - 95.1
Satellite/backpack ^e	Subadults and adult	4	-	33.7	58.9 - 98.5
Satellite/backpack ^c	Adult	1	-	60.2	94

^a As defined by [Ogren \(1989\)](#).

^b [Byles \(1988\)](#).

^c [Gitschlag \(1996\)](#).

^d [Morreale and Standora \(1998\)](#).

^e [Renaud \(1995\)](#).

Telemetric monitoring has demonstrated diel and seasonal shifts in the surface and submergence durations of Kemp's ridley turtles, but there are no distinct patterns among the few studies that have been conducted. Two radio-telemetered turtles in Chesapeake Bay exhibited longer surface durations during the day ([Byles, 1988](#)), although this observation was not tested statistically. Another turtle tracked via radio along the southeast U.S. coast exhibited significantly longer submergence durations at night (77.3 min) than during the day (13.7 min; [Gitschlag, 1996](#)). Satellite telemetry has indicated that average submergence durations of Kemp's ridley turtles were significantly higher during the night for all seasons (n=2; [Gitschlag, 1996](#)) and average submergence durations decreased in the spring (n=2; [Gitschlag, 1996](#)) and summer (n=4; [Renaud, 1995](#)). The numbers of submergences were higher during the day for both of these studies, but the seasonal patterns of submergence were opposite. Furthermore, the mean numbers of submergences reported by Renaud were approximately 7 times greater than those of Gitschlag. The differences between studies employing the same methodology is probably due to the individual variability among the few turtles tracked in each study. Intensive monitoring of a larger number of animals is needed to investigate the behavior of Kemp's ridley turtles.

Habitat Characterization

Characterizing the developmental habitats and determining the habitat utilization of Kemp's ridley turtles have been identified as priorities in the

conservation and management of this species ([Thompson et al., 1990](#); [U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992](#)). Subadult turtles typically inhabit coastal estuaries, and the biological and physical attributes of the areas in which they are caught have been used to characterize the habitats of this species. [Carr \(1942\)](#) first suggested that Kemp's ridley turtles preferred the red mangrove (*Rhizophora mangle*) habitat based on the observations of fishermen in southern Florida. [Carr and Caldwell \(1956\)](#) later noted that this species was also captured on seagrass (*Thalassia testudinum*, turtle grass, and *Syringodium filiforme*, manatee grass) shoals in the west-central Florida turtle fishery. [Ogren \(1989\)](#) identified mud, sand, oyster shell, and turtle grass as bottom types associated with the capture of subadult Kemp's ridley turtles. No preference for bottom type was indicated except those corresponding to portunid crab distribution (i.e. shallow seagrass beds and mud bottom bays of coastal marshes). [Rudloe et al. \(1991\)](#) compared the substrates (mud, sand, and seagrass) at the capture sites of subadult turtles in the northeastern Gulf of Mexico and detected no significant preference for bottom type. [Schmid \(1998\)](#) suggested that oyster reefs and mud bottom adjacent to the reefs were being preferentially utilized by Kemp's ridley turtles in west-central Florida.

Information gathered on the daily movements of Kemp's ridley turtles can also be used to characterize the habitat preferences of this species ([Timko and Kolz, 1982](#)). [Danton and Prescott \(1988\)](#) observed that a telemetered subadult turtle in Cape Cod Bay remained near a shallow-water shoal composed of extensive eelgrass (*Zostera marina*) flats. [Byles \(1988\)](#) also noted utilization of

shoal areas by two telemetered Kemp's ridley turtles in Chesapeake Bay and identified seagrass beds (*Z. marina* and *Ruppia maritima*) as the preferred habitat within their foraging ranges. As noted previously for behavioral studies, a larger number of turtles need to be tracked in order to characterize habitat associations via telemetric methods.

All of the aforementioned studies have inferred habitat preferences by Kemp's ridley turtles, but they are actually implying habitat utilization from the observations at telemetry and capture locations (Thomas and Taylor, 1990). There have been no efforts to quantify the amount of time Kemp's ridley turtles spend utilizing their habitats, and none of the investigations to date have characterized or quantified all of the habitat types available to turtles within the respective study areas. Estimates of habitat availability and utilization are commonly used to determine the habitat preferences of terrestrial animal populations (White and Garrott, 1991) and such estimates should be used in characterizing the foraging habitats of Kemp's ridley turtles (Schmid, 1994).

Research Objectives

Tagging studies have demonstrated that the coastal waters of west-central Florida are an important developmental region for subadult Kemp's ridley turtles (Schmid, 1998). Despite the long-term tagging efforts, there have been no attempts to document the activities and behavior of Kemp's ridley turtles inhabiting these foraging grounds. Radio and sonic telemetry have been used extensively to analyze the local movements, site fidelity, and respiratory behavior

of Kemp's ridley turtles along the Atlantic coast. However, efforts to date have not demonstrated patterns for these activities or preference for a particular habitat type. The purpose of the present study is to investigate the activity patterns and habitat associations of Kemp's ridley turtles in the nearshore waters of the Cedar Keys. The objectives of this dissertation are as follows:

- (1) To determine the extent to which Kemp's ridley turtles exhibit fidelity to the Cedar Keys study area.
- (2) To determine if the movements of Kemp's ridley turtles are oriented with the direction of the prevailing tidal flow and if the rate of movement is correlated to the rates of tidal flow.
- (3) To determine if the rate of movement and respiratory activities of Kemp's ridley turtles change with respect to time of day, and to determine if these patterns are correlated with one another and body size.
- (4) To characterize the various benthic habitats available within the Cedar Keys study area.
- (5) To estimate the utilization of habitat types by Kemp's ridley turtles.
- (6) To determine if Kemp's ridley turtles are exhibiting habitat preference by utilizing particular habitat types and water depths at a greater proportion than available in the study area.

Chapter 2 provides an overview of the telemetric methodology used in the present study and examines the daily activities of Kemp's ridley turtles as outlined in objectives 1 - 3. Chapter 3 examines the association of Kemp's ridley turtles with the coastal-benthic habitats of the Cedar Keys area as summarized in

objectives 4 - 6. Chapter 4 provides a synopsis of Chapters 2 and 3, and presents recommendations for further research.

CHAPTER 2

ACTIVITY PATTERNS OF KEMP'S RIDLEY TURTLES

Knowledge of spatial patterns and movements is the first step in comprehending the ecology of a species and is a vital component in the conservation strategies for endangered wildlife populations ([Weatherhead and Hoysak, 1989](#)). With the exception of migratory and nomadic movements, most animals confine their activities to specific areas ([Winter, 1977](#)). These areas are commonly referred to as "home ranges," though there has been considerable debate concerning the interpretation of the home range concept and the methods used to delineate the area ([Harris et al., 1990](#); [White and Garrott, 1990](#)). Regardless of the definition or methodology, a home range is a spatially and temporally restricted area that an animal traverses while performing its normal activities.

Estimating the size, shape, and patterns of movement within the home range are important features in wildlife studies, particularly those concerned with foraging behavior and habitat selection. [McNab \(1963\)](#) demonstrated that the home range sizes of some mammalian species were strongly correlated with their body sizes, foraging strategies, and relative food densities. Larger animals expend more energy owing to their higher body mass, and, therefore, require a greater area in which to acquire this energy. Furthermore, "hunters" (carnivores, insectivores, frugivores, and granivores) utilize widely dispersed food resources

and tend to have larger home range sizes than "croppers" (herbivorous grazers and browsers) of similar mass that utilize more densely distributed food.

Environmental conditions may also influence the body size and home range relationship, though there are no clear trends ([McNab, 1963](#)).

Understanding patterns of animal movement requires information on the environmental conditions in which movement occurs, as rhythmic patterns in the natural environment are a major influence underlying the behavioral patterns of animals ([Nieuwolt, 1996](#)). Each species adapts to diel and seasonal changes in the physical factors of the environment, such as illumination and temperature, and these adaptations are reflected in the activity patterns of the species ([Gourley, 1979](#)). In vertebrate taxa, however, the biological advantages of rhythmic activity are often determined by secondary ecological factors such as predation and food acquisition ([Cloudsley-Thompson, 1961](#)).

Most studies of animal activity patterns have dealt with terrestrial species. Radio telemetry is commonly employed to describe the movements and activities of free-ranging animals, and these descriptions are then used to test for correlations between the observed behaviors and environmental conditions ([White and Garrott, 1990](#)). Since the advent of acoustical telemetry, behavioral studies in the aquatic environment have focused on fish ([Stasko and Pincock, 1977](#)). Marine fish commonly exhibit daily activity patterns in response to predictable changes in light and tidal cycles, and these patterns have adaptive significance with respect to bioenergetics and niche definition ([Colton and Alevizon, 1983](#); [Gruber et al., 1988](#); [Nixon and Gruber, 1988](#)). Similar activities

have been observed in marine turtles, but attention has focused on the seasonal, rather than the daily, influences of the environment.

For example, the Kemp's ridley turtle, *Lepidochelys kemp*, is the most endangered species of marine turtle and is distributed throughout the Gulf of Mexico and northwestern Atlantic Ocean. Tagging studies have been conducted in U.S. coastal waters to characterize regional aggregations of subadult turtles and to investigate their movements and migrations. Recaptures along the Atlantic coast have indicated a seasonal north-south migration. Turtles tagged off the Florida east coast during the winter have been recaptured in northeastern waters during the summer, and turtles tagged in northeastern waters in summer have been recaptured off Florida in the winter (Henwood and Ogren, 1987; Schmid, 1995). Mark-recapture data along the northern Gulf coast have demonstrated east-west movements (Carr, 1980; Ogren, 1989), but there are no recoveries that indicate a seasonal migration. Short-term recaptures at sites of initial capture have demonstrated fidelity to specific areas (Schmid, 1995; Musick and Limpus, 1997; Morreale and Standora, 1998), while long-term and multiannual recaptures have indicated that some turtles remigrate to capture sites and may do so for at least 4 years (Schmid, 1998). However, recoveries of tagged turtles only reveal endpoints and periodicities of migration or movement, and yield little information on their behavior between capture and recapture (Carr, 1980; Meylan, 1982).

Telemetric techniques have been used to investigate the activities of Kemp's ridley turtles, and thus fill the data gaps of tagging studies, but the primary goal of most studies has been to describe patterns of movement and

migration. Satellite transmitters have been used to document southward migration from New England waters during the fall ([Standora et al., 1992](#); [Morreale and Standora, 1998](#)), overwintering off the east-central coast of Florida and northward remigration in the spring ([Renaud, 1995](#); [Gitschlag, 1996](#)), and west-east migration in northern Gulf coastal waters ([Renaud, 1995](#)). Radio and sonic transmitters have been applied to investigate tidal orientation in Chesapeake Bay ([Byles, 1988](#)), diving patterns and seasonal movement patterns in Long Island Sound ([Standora et al., 1990](#); [Morreale and Standora, 1998](#)), departure from inshore waters of New York during the fall ([Standora et al., 1990](#); [Morreale and Standora, 1998](#)), and southward movements along the east coast of Florida during the winter ([Gitschlag, 1996](#)).

A few investigators have employed radio and sonic telemetry to describe the localized movements and short-term site fidelity of Kemp's ridley turtles in coastal estuaries ([Byles, 1988](#); [Danton and Prescott, 1988](#); [Morreale and Standora, 1998](#)), but only [Renaud and Williams \(1997\)](#) have conducted home range analyses for this species. Studies of Kemp's ridley behavior have focused on seasonal and diel patterns of surface and submergence durations ([Byles, 1988](#); [Renaud, 1995](#); [Gitschlag, 1996](#)). However, these efforts have produced insufficient and conflicting results owing to differences in the methodologies employed, small numbers of turtles tracked in each study, and individual variation by the few turtles tracked to date.

The eastern Gulf of Mexico, particularly the Cedar Key area of western Florida, has been identified as an important developmental region for Kemp's

ridley turtles (Bjorndal and Bolten, 1990; Thompson et al., 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). However, relatively little is known about the activities of turtles in this area other than anecdotes from fishermen and observations from mark-recapture studies (Carr and Caldwell, 1956; Schmid and Ogren, 1990, 1992; Schmid, 1998). Discerning daily activity patterns and factors influencing these patterns would not only benefit conservation and management efforts for this highly endangered species, but would also provide insight into the ecological roles of Kemp's ridley turtles in coastal habitats (Bjorndal and Bolten, 1990; Thompson et al., 1990). The purpose of the present study is to provide information on the site fidelity, movements, and respiratory behavior of Kemp's ridley turtles in the coastal waters of the Cedar Keys, Florida, and to test hypotheses concerning tidal orientation and diel patterns of movement and respiration.

Predictions and Hypotheses

1. Carr and Caldwell (1956) tagged and released Kemp's ridley and green turtles (*Chelonia mydas*) obtained from Cedar Key fish houses, and noted that a few turtles returned to the area where they had been originally captured within a short period of time. The authors suggested that these turtles were exhibiting homing behavior and were establishing home ranges during their seasonal occurrence in the nearshore waters of western Florida. Kemp's ridley turtles captured and tagged in the Cedar Keys have been recaptured at initial capture sites both within and between seasons, prompting Schmid and Ogren (1990,

1992) to conclude that these turtles were seasonal residents with restricted home ranges. I predict Kemp's ridley turtles will occupy well-defined foraging ranges in the Cedar Keys study area and will exhibit fidelity to specific sites within the study area.

2. Byles (1988) indicated that the movements of loggerhead turtles (*Caretta caretta*) were strongly influenced by the tidal cycle, whereas Kemp's ridley turtles did not range as far with the tide. However, my communications with fishermen in the Cedar Keys and personal field observations in this area suggest that Kemp's ridley turtles are moving with the prevailing tidal current. I will test the null hypothesis that the direction of movement of Kemp's ridley turtles is uniformly distributed during each tidal state. If turtles do exhibit significant tidal orientation, I predict their rate of movement will increase with increasing tidal velocity.

3. Most species of turtles are generally active during the day (diurnal), though some also perform nighttime (nocturnal) activities such as nesting (Cloudsley-Thompson, 1961; Gourley, 1979). Patterns of diurnal foraging and nocturnal resting have been observed in subadult green (Mendonça, 1983) and hawksbill turtles (*Eretmochelys imbricata*; van Dam and Diez, 1998), but these patterns were not evident for subadult Kemp's ridley and loggerhead turtles (Byles, 1988). Increased diurnal movements (Standora et al., 1989) and increased crepuscular (sunrise and sunset) dive frequencies (Morreale and Standora, 1998) have been suggested for Kemp's ridley turtles, but the authors did not provide quantitative data to substantiate their inferences. I will test the null

hypothesis that the rate of movement and respiratory activities of Kemp's ridley turtles are equally distributed throughout the 24-hour cycle.

4. Laboratory experiments have demonstrated an increase in respiratory frequency from induced swimming in captive loggerhead ([Lutz et al., 1989](#)) and green turtles ([Butler et al., 1984](#); [West et al., 1992](#)). Resting turtles surfaced intermittently to breathe, with one or more breaths per episode, followed by longer submerged periods. Swimming turtles established a more continuous pattern of surfacing to breathe. Regardless of the activity, there is a tendency for the number of breaths per breathing episode to increase with submergence time ([Lutcavage and Lutz, 1997](#)), therefore increasing the duration at the surface. I predict the frequency of respiratory surfacings will increase, and the surface and submergence durations will decrease, with increasing rate of movement in free-ranging Kemp's ridley turtles.

5. The size of the home range areas of mammalian ([McNab, 1963](#); [Gittleman and Harvey, 1982](#)) and avian species ([Schoener, 1968](#)) have been positively correlated with their body mass. This relationship has also been demonstrated for green turtles foraging in a lagoonal habitat ([Mendonça, 1983](#)). No such correlation has been demonstrated for Kemp's ridley turtles, but [Ogren \(1989\)](#) suggested that smaller turtles are restricted to shallower water depths and shorter dive durations owing to their higher metabolic rate and reduced lung capacity. I predict that the home range area and respiratory durations of Kemp's ridley turtles will increase with increasing carapace length and mass.

Materials and Methods

Data Collection

Study area

The study was conducted in Waccasassa Bay, which is located on the west coast of Florida and east of the Cedar Keys ([Fig. 2-1](#)). The northern and eastern boundaries of Waccasassa Bay are delineated by undeveloped saltmarsh coastline. The Waccasassa River drains into the northeastern region and is the major contributor of freshwater to this estuarine embayment ([Wolfe, 1990](#)). Research efforts were concentrated in the western portion of the bay, which is bordered by the Cedar Keys archipelago and the fishing community of Cedar Key. The southern region is open to the marine waters of the Gulf of Mexico. The two prominent geographic features within Waccasassa Bay are Corrigan Reef, a series of oyster and shell bars located in the northwestern region, and Waccasassa Reefs, three parallel seagrass shoals in the eastern half of the bay.

Capture of marine turtles

A large-mesh entanglement net (65 m length, 51 cm stretch mesh, and 20 meshes deep) was used to capture Kemp's ridley turtles near Corrigan Reef. The net was set in areas of aggregation identified by [Schmid \(1998\)](#) and retrieved upon capture of a turtle. Straight-line carapace length (SCL; nuchal notch to tip of

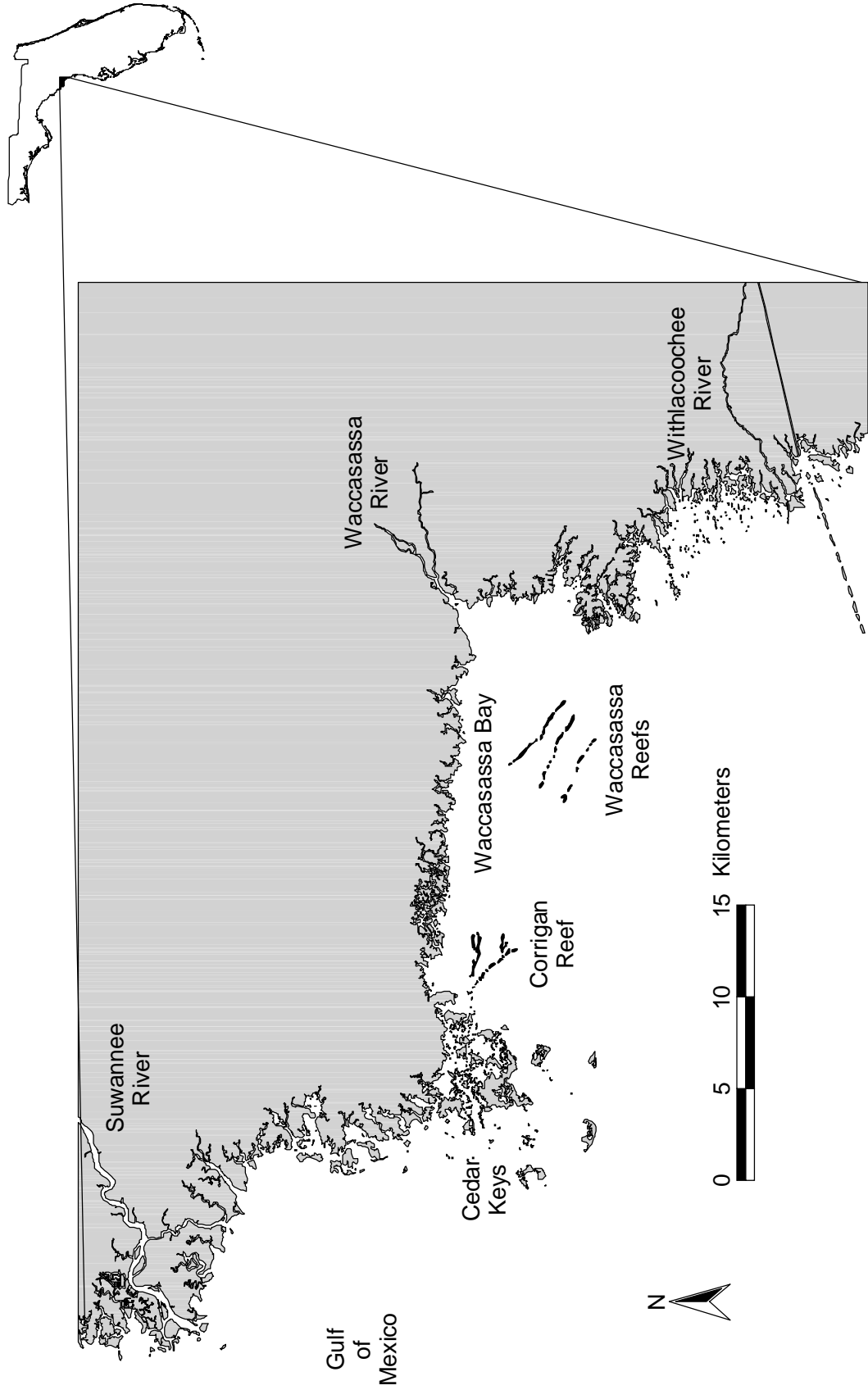


Figure 2-1. Map of west-central Florida showing the Cedar Keys study area.

postcentral scutes) was measured to the nearest 0.1 inch with forester's calipers, and mass was measured to the nearest 0.25 lbs with a spring scale.

Measurements were converted to metric for analyses owing to the measurement scales of the available instruments. Turtles were tagged with an Inconel tag on each fore flipper and a passive integrated transponder (PIT) tag was inserted in the left front flipper. Turtles were held on board the tracking vessel for less than 5 hours prior to release.

Radio and sonic telemetry

Each turtle was instrumented with a CHP-87-L sonic transmitter (Sonotronics, Tucson, AZ) and a MOD-050 radio transmitter with a TA-7 antenna (Telonics, Mesa, AZ). Sonic transmitters (32-44 kHz range with constant or coded pulse interval) were attached to posterior marginal scutes. Stainless steel wire was looped through the ends of the transmitter and plastic ties were inserted through the loops and through holes drilled in the scutes. Sonic transmitters were monitored with a N30A5B directional hydrophone and receiver (Dukane Corp., St. Charles, IL). Buoyant radio transmitters (164-165 MHz band) were attached to one of the postcentral marginal scutes by a 0.2 cm diameter monofilament tether with a breakaway link (S. Morreale and E. Standora, pers. comm.). Tether length was approximately two-thirds the carapace length of a turtle, so that the tether would not tangle in the fore flippers and the turtle was unable to bite the transmitter. Radio transmitter floats were constructed from SH model Ecofoam (128 kg/m^3 ; Deanco Inc., Winter Park, FL). Floats were painted

grey or black to decrease detection by predators (i.e., sharks) and coated with an epoxy resin to reduce damage. Radio transmitters were monitored with a CE12 receiver (Custom Electronics of Urbana, Inc., Urbana, IL) connected to a directional six-element Yagi antenna (Cushcraft Corp., Manchester, NH). The radio antenna was mounted on a rotating mast approximately 3 m above the sea surface.

Tracking protocol

Radio monitoring and sonic tracking were conducted from an 8.5 m wooden hull vessel with an inboard engine. Telemetered turtles were released in the area of capture, and tracking began after a 24-hour acclimation period. Tracking was conducted opportunistically in 1994, and most data were collected during the day. In 1995, turtles were systematically monitored for 4 tracking intervals of approximately 12 hours each, so that observations were collected each hour over two 24-hour cycles. At least 24 hours elapsed before initiating the second tracking interval, at least 48 hours elapsed before initiating the third interval, and at least 24 hours elapsed before initiating the fourth interval. After the intensive tracking period, turtles were located opportunistically to establish their presence in the study area. Intensive tracking efforts were abandoned if a turtle traveled more than 6 km from South Bar Light located south of Corrigan Reef ([Fig. 2-2](#)).

Radio telemetry was used to monitor surface times and durations (number of pulses) of turtles and to obtain bearings for long distance tracking. Sonic

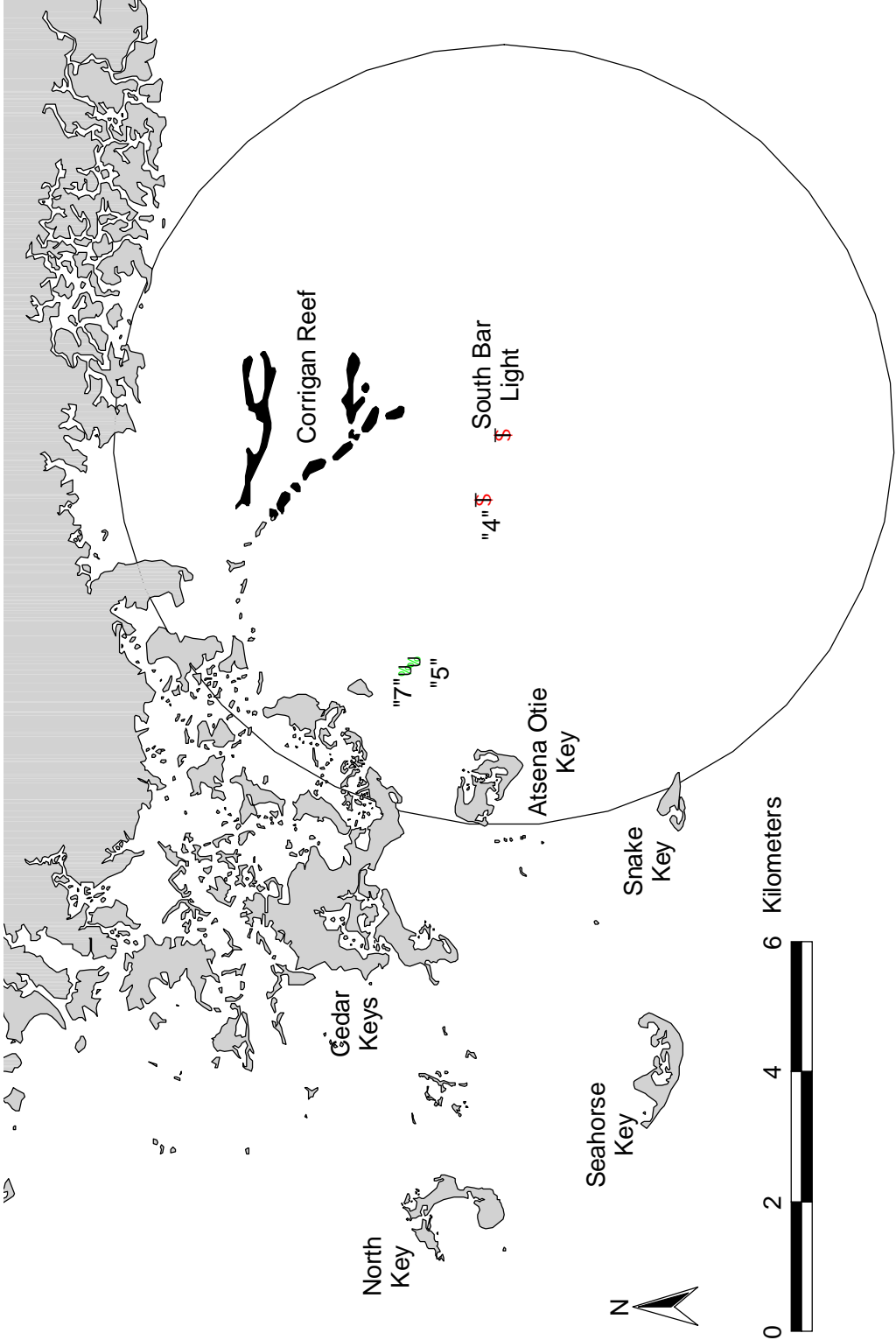


Figure 2-2. Map of the tracking area (large circle) for Kemp's ridley turtles and the Cedar Keys archipelago. Squares and triangles represent channel markers.

telemetry was used to pinpoint the location of turtles and to track their movements. Turtle locations were recorded hourly by homing-in on the sonic signal and maneuvering the tracking vessel within 10 - 20 m of the turtle. Distances were assessed by sighting a turtle and noting the strength of the sonic signal at 1/2 gain on the receiver. Turtle locations were estimated from the Universal Transverse Mercator (UTM) coordinates of the tracking vessel using a Global Positioning System (GPS, NAV 5000DX with software upgraded to NAV 5000DLX, Magellan Systems Corp., San Dimas, CA) with differential correction. Accuracy of the locational estimate was approximately 5 m as determined from the variability associated with a fixed position. The tracking vessel was anchored in the vicinity of a telemetered turtle between acquisition of locations. Direction of tidal flow at each turtle location was determined by observation in 1994 and with a handheld compass in 1995. Tidal flow rate was measured in 1995 by lowering a weighted flowmeter (Serial #B, General Oceanics, Miami, FL) approximately 1 m below the surface and recording the number of revolutions per second within a 30-second period.

Data Analysis

Site fidelity

Site fidelity was determined from the tendency of animals to remain within the Cedar Keys area and to maintain a stable home range size. The minimum area method of home range estimation ([Ackerman et al., 1990](#); [White and](#)

Garrott, 1990) was used to define the total area utilized by a telemetered turtle. A convex polygon was constructed by connecting the outer locations so that the internal angles of the polygon did not exceed 180 degrees. The computer program HOME RANGE (Ackerman et al., 1990) was used to calculate the UTM coordinates and area (km²) of each turtle's home range polygon and the distances (m) traveled between consecutive locations.

Tidal orientation

Relative distances in the x (ΔX) and y (ΔY) directions were determined between consecutive locations of each turtle

$$\Delta X = x_{i+1} - x_i$$

$$\Delta Y = y_{i+1} - y_i$$

where x_i is the north UTM coordinate and y_i is the east UTM coordinate for location i . The angle (a_i) in degrees between locations was calculated as

$$a_i = \begin{cases} \arctan(\Delta Y / \Delta X)(180^\circ / \pi) & \text{if } \Delta X > 0 \\ 180^\circ + \arctan(\Delta Y / \Delta X)(180^\circ / \pi) & \text{if } \Delta X < 0 \\ 90^\circ & \text{if } \Delta X = 0 \text{ and } \Delta Y > 0 \\ 270^\circ & \text{if } \Delta X = 0 \text{ and } \Delta Y < 0 \end{cases}$$

Angles were converted to bearings (b_i) with the formula

$$b_i = 90 - a_i$$

and 360° was added if the resulting value was negative (left of true north).

Directional data for each turtle were pooled respective to the tidal phase (incoming or falling) in which they occurred. Mean rectangular coordinates were computed for the pooled tidal phases of each turtle

$$\bar{X} = \frac{1}{n}(\sum \cos a_i)$$

$$\bar{Y} = \frac{1}{n}(\sum \sin a_i)$$

Length of the mean vector (r) is a measure of concentration for the sample of angles and was calculated for the pooled tidal phases of each turtle

$$r = \sqrt{\bar{X}^2 + \bar{Y}^2}$$

When $r=0$, the mean angle (\bar{a}) is undefined (no concentration or multimodal angles), and when $r \neq 0$, \bar{a} is determined by

$$\bar{a} = \begin{cases} \arctan(\bar{Y} / \bar{X})(180^\circ / \pi) & \text{if } \bar{X} > 0 \\ 180^\circ + \arctan(\bar{Y} / \bar{X})(180^\circ / \pi) & \text{if } \bar{X} < 0 \\ 90^\circ & \text{if } \bar{X} = 0 \text{ and } \bar{Y} > 0 \\ 270^\circ & \text{if } \bar{X} = 0 \text{ and } \bar{Y} < 0 \end{cases}$$

Mean angles were converted to mean bearings (\bar{b}) as described for individual angles. Angular deviation (s) was calculated with the formula

$$s = 180^\circ / \pi \sqrt{-2 \ln r}$$

Rate of movement and tidal speeds

Rate of movement (*ROM*) in km/hr was calculated as

$$ROM = \frac{d_i / 1000}{t_i / 60}$$

where d_i is the distance in meters between two consecutive locations and t_i is the time in minutes between locations. Using the conversion chart on the flowmeter, tidal speed (*T*) in km/hr was calculated as

$$T = 0.096(F)$$

where F is the measured flow rate in revolutions/second.

Respiratory behavior

The radio transmitters emit 50 pulses per minute or one pulse every 1.2 seconds. Surface duration was calculated by multiplying the recorded number of pulses by 1.2 seconds. Submergence duration was estimated by the number of minutes elapsed from the beginning of the previous radio contact minus the corresponding surface duration. Rates of movement and surface/submergence durations were pooled for all turtles, by year tracked, and for each turtle by time of day (Eastern Standard Time) using the two level time intervals [0800-1959 h (day) and 2000-0759 h (night)] of [Renaud \(1995\)](#) and four level time intervals [0500-0859 h (dawn), 0900-1659 h (day), 1700-2059 h (dusk), and 2100-0459 h

(night)] of [Renaud et al. \(1995\)](#). Surface durations, submergence durations, and number of surfacings were also pooled within the time intervals of consecutive locations for correlation analyses.

Statistical methods

A basic assumption in most statistical analyses of animal movements is the independence between successive locations collected during telemetric monitoring. Locational data collected via telemetry are considered independent if an animal's current position is not a function of its previous positions ([Swihart and Slade, 1985 a,b](#); [White and Garrott, 1990](#)). The time to independence has been described as the time necessary for an animal to traverse its home range ([Swihart and Slade, 1985a](#)) or a statistically significant part of its home range ([Ackerman et al., 1990](#)). However, minimum time interval to statistical independence can be long enough to eliminate information of biological significance ([Andersen and Rongstad, 1989](#); [Reynolds and Laundré, 1990](#); [McNay et al., 1994](#)). The length of time necessary for statistically independent data can produce inaccurate estimates of daily distances traveled and activity patterns since these behaviors often require a short sample period ([Reynolds and Laundré, 1990](#)). Data collection at short, systematic intervals are needed to maximize the behavioral information available from telemetry studies, despite the violation of the independence assumption ([Reynolds and Laundré, 1990](#); [McNay et al., 1994](#)). Therefore, hourly sampling intervals were selected in order to quantify the behavioral trends of Kemp's ridley turtles foraging in the Cedar Keys

area, despite the possibility of autocorrelated data. Efforts were made to use statistical analyses that did not require the assumption of independent observations, but this was not always possible. The computer program HOME RANGE ([Ackerman et al., 1990](#)) was used to calculate three indices of serial (auto-) correlation: t^2/r^2 ([Swihart and Slade, 1985a](#)), Ψ (psi; [Swihart and Slade, 1985b](#)), and γ (gamma; [Swihart and Slade, 1986](#)). These indices were applied to 1, 2, 4, and 6 hour intervals between successive locations of each turtle in order to determine the minimum time to independence.

[Batschelet \(1981\)](#) suggested combining descriptive circular statistics for each individual to create a second-order sample of mutually independent data pairs. The mean bearings and mean vector lengths of each turtle were combined to create a second-order sample of polar coordinates for each tidal phase. The number of first-order observations for each individual must be equal in order for the second-order data pairs to have the same weight, although slight departures will not severely affect results. Since the tidal orientation data have unequal sample sizes, it was assumed that the data pairs for each turtle had equal weights. The V test ([Batschelet, 1981](#)) was used to test whether the mean bearings of the turtles were clustered around the bearings of the incoming and falling tides. Tidal bearings collected during 1995 were used to calculate mean bearings for the incoming tides and the falling tides.

Distributions of variables (rates of movement and surface and submergence durations) were tested with the Shapiro-Wilk test for normality. Homogeneity of variances was tested with the F-test for two level time intervals

and Bartlett's test for homogeneity for four level time intervals. The Kruskal-Wallis analysis was used to test for differences in means of the variables in the absence of normality and/or nonhomogeneity of variances. Statistical significance was accepted at $P < 0.05$. When a significant difference between four level time intervals was detected and parametric assumptions had been violated, a nonparametric multiple comparison procedure described by [Daniel \(1990\)](#) was used to determine which means differed at $\alpha = 0.05$. Although the use of the rate of movement and surface-submergence data as the sample unit to compare across animals is pseudoreplication ([Otis and White, 1999](#)), these analyses were performed to describe individual variability and to compare results with previous studies. Spearman correlation coefficient was used to determine the correlations among rates of movement, mean hourly surface and submergence durations, and number of surfacings per hour for all turtles combined, by year tracked, and for each turtle. Spearman correlation coefficient was also used to determine the correlations between the body size (carapace length and mass) and the home range area, mean rate of movement, mean number of surfacings, mean surface duration, and mean submergence duration of each turtle.

Results

Equipment Performance

Adverse weather conditions were a major limitation to telemetric monitoring. Radio transmitters had a range of approximately 8 km given the height (3 m) of the receiving antenna above sea level. Interference with the reception of radio signals included the GPS antenna, electrical engine noise, lightning discharge, and unidentified radio transmissions. The range of the radio signals was also a function of the height of the transmitter antenna above the water's surface, which was affected by the buoyancy of the transmitter and the sea state. Four detached radio transmitters (2 with broken tether swivels and 2 with disconnected breakaway links) were recovered within 5-24 days after application. Transmitters recovered 2-3 weeks after attachment had become fouled by barnacles and hydrozoa.

Sonic transmitters were detected at distances up to 1 km under good conditions and less than 100 m under poor conditions. Recognizable factors affecting reception of the sonic signal include sea state, tidal flow, bottom topography and substrate, marine organisms, and propeller wash. Two detached sonic transmitters were recovered during the study and both displayed abrasions and indentations on the surface.

Telemetry Overview

Five Kemp's ridley turtles were instrumented with transmitters from May to August 1994, and ten turtles were instrumented from May to November 1995. Of this total, only turtles with > 40 hours radio monitoring or > 40 locations were used in the analyses of activity patterns ([Table 2-1](#)). Turtles not included either lost their transmitters prematurely or moved out of the study area (see [Site Fidelity](#) section of Results). Carapace lengths for turtles used in the analyses ranged from 35 to 54 cm SCL and mass ranged from 6 to 23 kg. The total mass of the telemetry array applied to the turtles was approximately 105 g (radio transmitter \approx 58 g, tether \approx 11 g, and sonic transmitter \approx 36 g), which was less than 2% of the mass of the smallest turtle ([Table 2-1](#)).

A minimum time to independence of 4-6 hours was obtained by calculating the indices of autocorrelation between successive observations ([Table 2-2](#)). The results of this analysis should be interpreted cautiously given the reduction in sample size by deleting observations and the decreasing number of consecutive locations with increasing time intervals. The observed time to independence may be the result of the six hour duration of each tide in the Cedar Keys area. If turtle movements were correlated with tidal flow, a turtle would traverse its home range during a 6 hour tidal period. [Krebs \(1989\)](#) noted that ecological estimates could be biased if the sampling interval of a systematic sample corresponds with a periodic trend in environmental conditions. Sampling turtle locations at the peak high and low tides may produce a bimodal distribution of locational data, whereas

Table 2-1. Summary of Kemp's ridley turtles tracked by radio and sonic telemetry at the Cedar Keys, Florida.

Tag code	Turtle ID	Carapace length (cm)	Mass (kg)	Contact duration	Hours monitored (radio)	Number of locations (sonic)	Convex polygon (km ²)
1994 season							
PPY 168 – 169 ^a	LK1	43.4	11.8	5/30 - 7/15	48.8	69	5.82
PPY 172 – 173 ^b	LK2	54.0	23.1	6/19 - 7/01	43.8	47	12.89
PPY 175 – 176 ^c	LK3	46.2	14.1	7/09 - 7/26	16.2	50	29.51
PPY 177 – 178 ^d	LK4	36.6	7.7	8/01 - 8/27	59.1	53	11.40
1995 season							
PPY 183 – 184	LK5	41.9	11.3	5/04 - 6/15	16.5	57	25.85
PPY 185 – 186 ^e	LK6	46.0	13.4	5/22 - 7/27	58.8	65	17.97
PPY 191 – 192 ^f	LK7	49.9	19.0	6/19 - 7/24	55.8	59	19.74
PPY 195 – 196	LK8	34.7	5.9	7/14 - 9/22	54.2	58	6.66
PPY 197 – 198 ^g	LK9	49.3	16.3	8/05 - 8/19	51.2	54	4.92

^a Originally tagged 10/3/91, recaptured 9/20/92, and recaptured 5/2/94. Missing distal ends of rear flippers.

^b Notches in marginal scutes (resembling mating scars?).

^c Large notch in left marginal scutes.

^d Large notch in left marginal scutes.

^e Notches in right marginal and left postcentral scutes. Missing distal end of right rear flipper.

^f Large notch in right marginal scutes. Lacerated distal end of right rear flipper.

^g Originally tagged 1991 (marginal mark), recaptured 9/19/93, and recaptured 8/5/95. Notches in right marginal and postcentral scutes.

Table 2-2. Indices of serial correlation for determining the time to independence of Kemp's ridley turtle locational data. * - significant ($p < 0.05$) autocorrelation, ns – no significant autocorrelation.

Turtle ID	Hourly interval	Indices of serial correlation		
		t^2/r^2	Ψ	γ
LK1	1	0.34 *	2.59 *	0.83 *
	2	0.69 *	2.10 *	0.65 *
	4	1.13 *	1.52 *	0.35 ns
	6	1.19 *	1.09 *	0.27 ns
LK2	1	0.41 *	2.25 *	0.77 *
	2	0.75 *	1.79 *	0.58 *
	4	0.67 *	1.91 *	0.49 *
	6	1.28 *	1.13 *	0.16 ns
LK3	1	0.23 *	2.48 *	0.85 *
	2	0.48 *	1.91 *	0.67 *
	4	0.94 *	1.20 *	0.34 *
	6	1.45 *	0.66 ns	0.08 ns
LK4	1	0.40 *	1.71 *	0.78 *
	2	0.82 *	1.15 *	0.56 *
	4	1.36 *	0.69 *	0.18 ns
	6	1.58 *	0.07 ns	-0.04 ns
LK5	1	0.26 *	2.26 *	0.85 *
	2	0.55 *	1.95 *	0.70 *
	4	1.04 *	1.55 *	0.44 *
	6	1.77 ns	0.80 *	0.05 ns
LK6	1	0.22 *	2.42 *	0.84 *
	2	0.46 *	1.98 *	0.66 *
	4	0.86 *	0.97 *	0.31 *
	6	1.26 *	0.45 ns	0.13 ns
LK7	1	0.32 *	2.55 *	0.84 *
	2	0.63 *	2.21 *	0.68 *
	4	1.23 *	1.36 *	0.37 *
	6	1.54 *	0.87 *	0.21 ns
LK8	1	0.16 *	2.29 *	0.90 *
	2	0.29 *	1.93 *	0.79 *
	4	0.64 *	1.20 *	0.51 *
	6	1.08 *	0.85 *	0.21 ns
LK9	1	0.17 *	3.02 *	0.87 *
	2	0.42 *	2.60 *	0.70 *
	4	0.92 *	1.47 *	0.41 *
	6	0.97 *	1.33 *	0.34 *

sampling at mid-tide may yield a cluster of locations in the center of the actual home range.

Site Fidelity

Of the 15 Kemp's ridley turtles instrumented with transmitters, only one turtle was not located for subsequent tracking. This turtle may have left the Cedar Keys study area or its radio transmitter may have failed and sonic contact could not be re-established due to the limited range of this latter method. Four Kemp's ridley turtles left the tracking area and were not included in the analyses owing to insufficient data. One turtle traveled over 8 km to the east-southeast of South Bar Light, possibly to Waccasassa Reefs, and returned to the study area 7 days later. Two other turtles traveled approximately 7.5 km to the west-southwest of South Bar Light to an unnamed ship channel. One of these turtles was tracked leaving the study area through the channel separating the Cedar Keys and Atsena Otie Key ([Fig. 2-2](#)). Both turtles were located in the vicinity of Corrigan Reef 2 - 3 days later. The turtle that was tracked westward was located near South Bar Light over a two month period before being recaptured and re-instrumented, and was at large for a total of 93 days. The fourth turtle traveled approximately 7 km to the south after the passage of a cold front in late October 1995 and remained in this area for another two weeks before contact was lost.

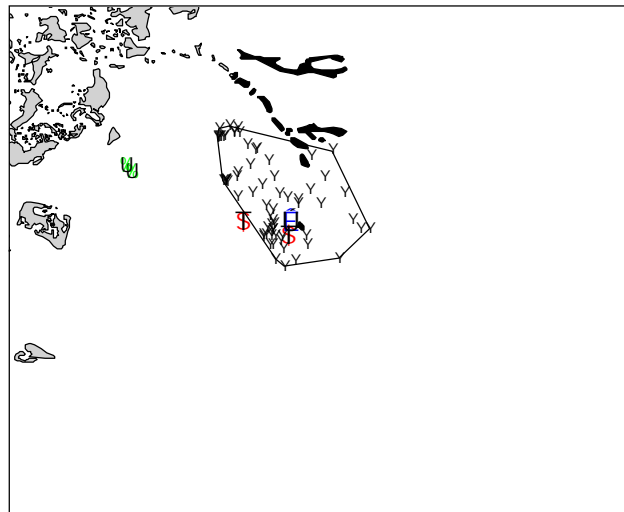
Kemp's ridley turtles used in activity pattern analyses were located in the Cedar Keys study area up to 66 days after initial capture ([Table 2-1](#)). The locations of six of the turtles were aggregated within 4.25 km of Corrigan Reef

and the channel markers (Marker #4 and South Bar Light) south of the reef (Fig. 2-3). The other three turtles were located between 1.2 - 6.25 km to the south and east of the reef and markers (Fig. 2-3). Two turtles (LK1 and LK9) were recaptures from previous tagging studies at Corrigan Reef and had been at large for 3 - 4 years prior to telemetric monitoring (Table 2-1). These turtles and three others (LK2, LK4, and LK8) occupied 4.9 - 12.9 km² home range areas with a gradual increase in size during their respective monitoring periods (Fig. 2-4). In contrast, four turtles (LK3, LK5, LK6, and LK7) occupied 18.0 - 29.5 km² home range areas with periodic increases of 10 - 20 km² in home range size (Fig 2-4). Home range area was not significantly correlated with carapace length or mass (Spearman corr. coeff.=0.17, p=0.67).

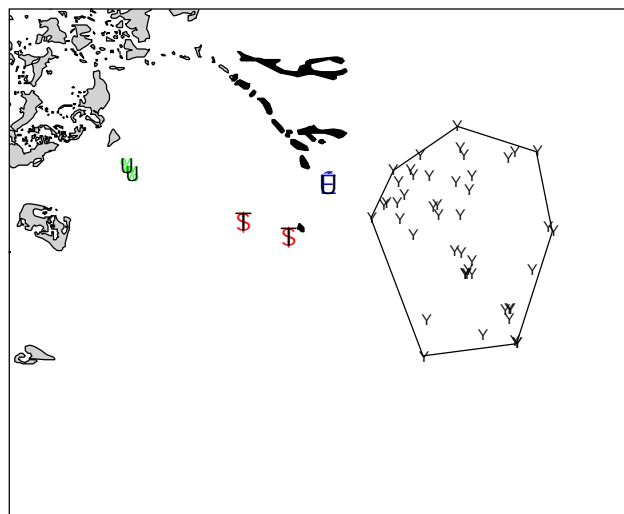
Tidal Orientation

The mean of mean turtle bearings was $48 \pm 49^\circ$ for incoming tides and $232 \pm 41^\circ$ for falling tides (Table 2-3). The mean tidal bearings for 1995 were $37 \pm 9^\circ$ ($r=0.9879$, $n=113$) for incoming tides and $234 \pm 9^\circ$ ($r=0.9867$, $n=149$) for falling tides. The second-order samples of turtle bearings differed significantly from randomness for both the incoming tides ($u=2.90$, $0.001 < p < 0.0025$) and the falling tides ($u=3.30$, $p < 0.005$), indicating that the mean bearings of turtles were clustered around the mean bearings of the tidal states (Fig. 2-5).

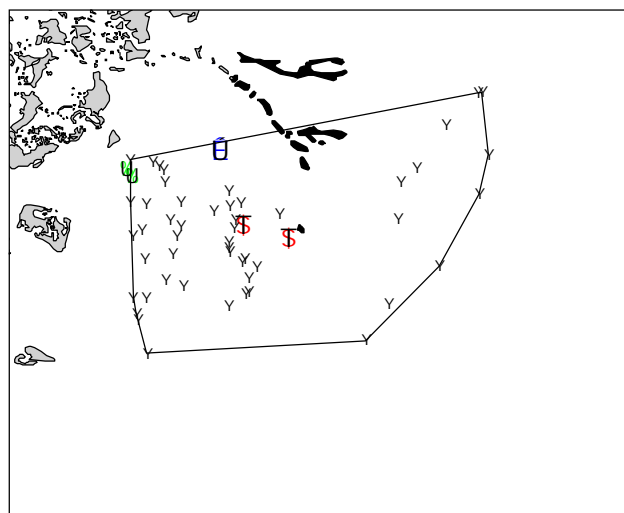
Mean vector lengths were low for incoming tides (Table 2-3) and mean angular deviations ranged from 69° to 134° . Mean vector lengths for falling tides were relatively higher, indicating an increased concentration of bearings, and



LK1
5.82 km²

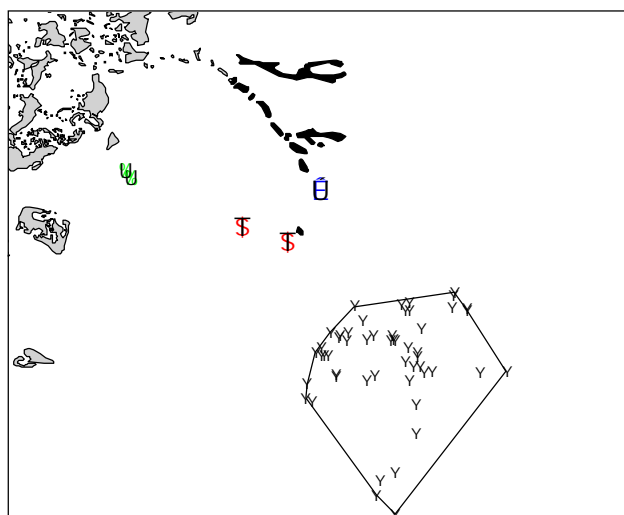


LK2
12.89 km²

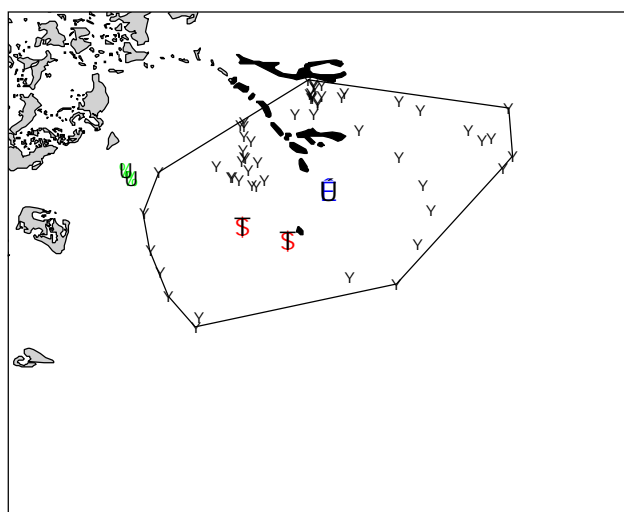


LK3
29.51 km²

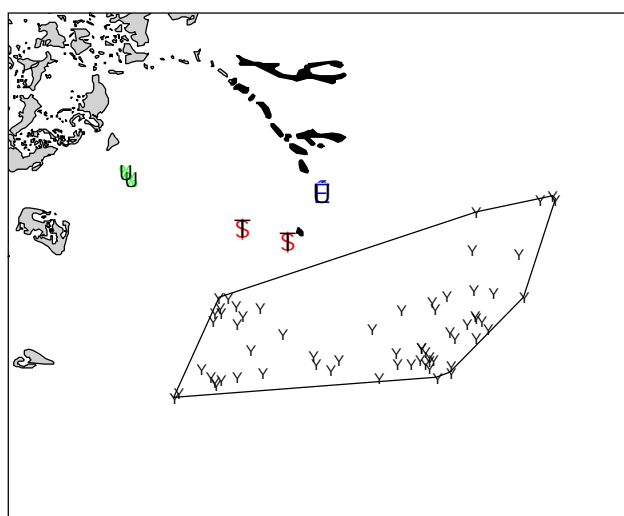
Figure 2-3. Locations and home ranges of Kemp's ridley turtles relative to Corrigan Reef (black polygons). Squares and triangles represent channel markers and stars denote the release site of each turtle. Numbers indicate the total area of the home range.



LK4
11.40 km²

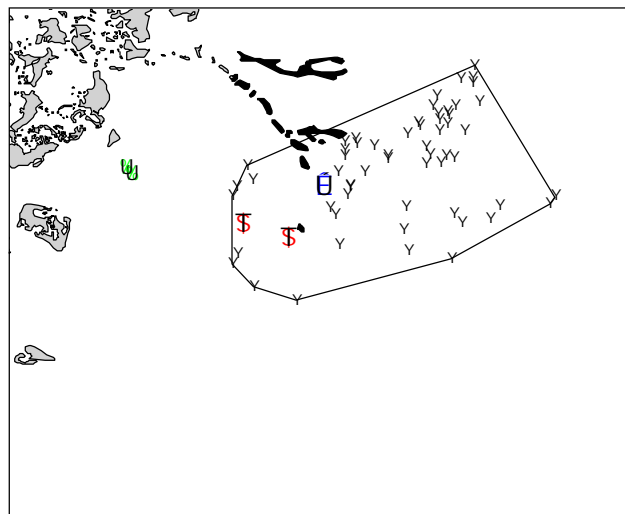


LK5
25.85 km²

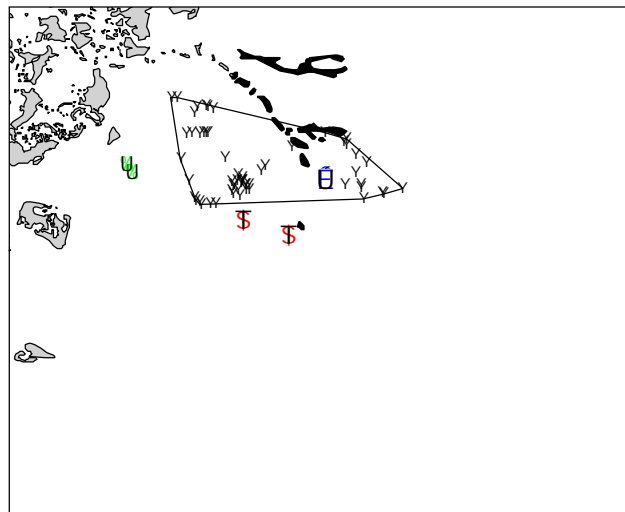


LK6
17.97 km²

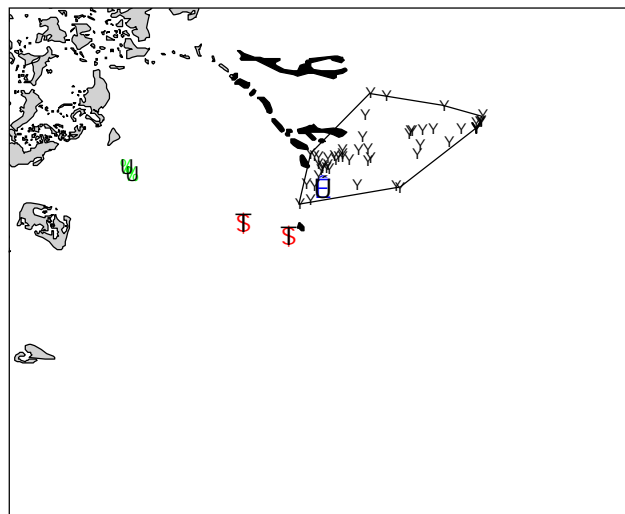
Figure 2-3. continued.



LK7
19.74 km²



LK8
6.66 km²



LK9
4.92 km²

Figure 2-3. continued.

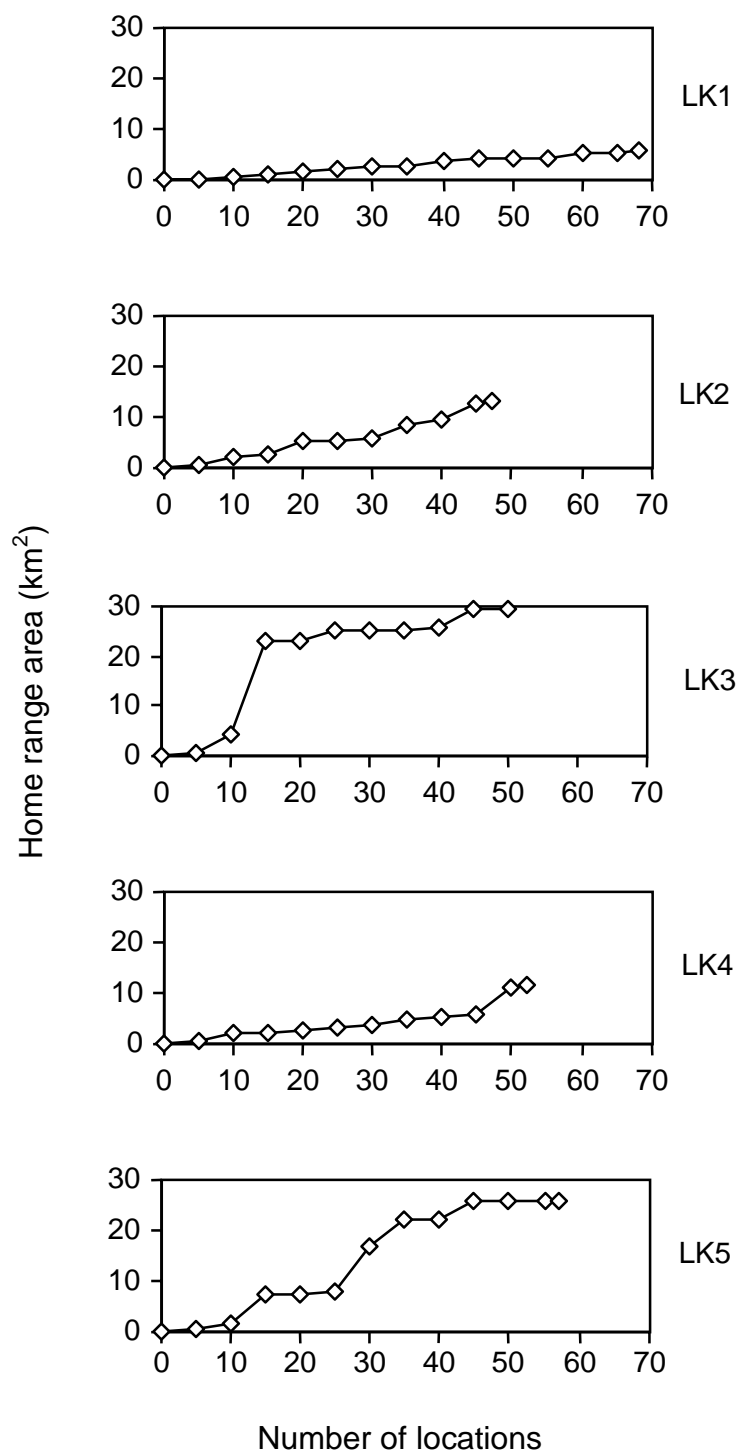


Figure 2-4. Home range area versus number of locations for Kemp's ridley turtles.

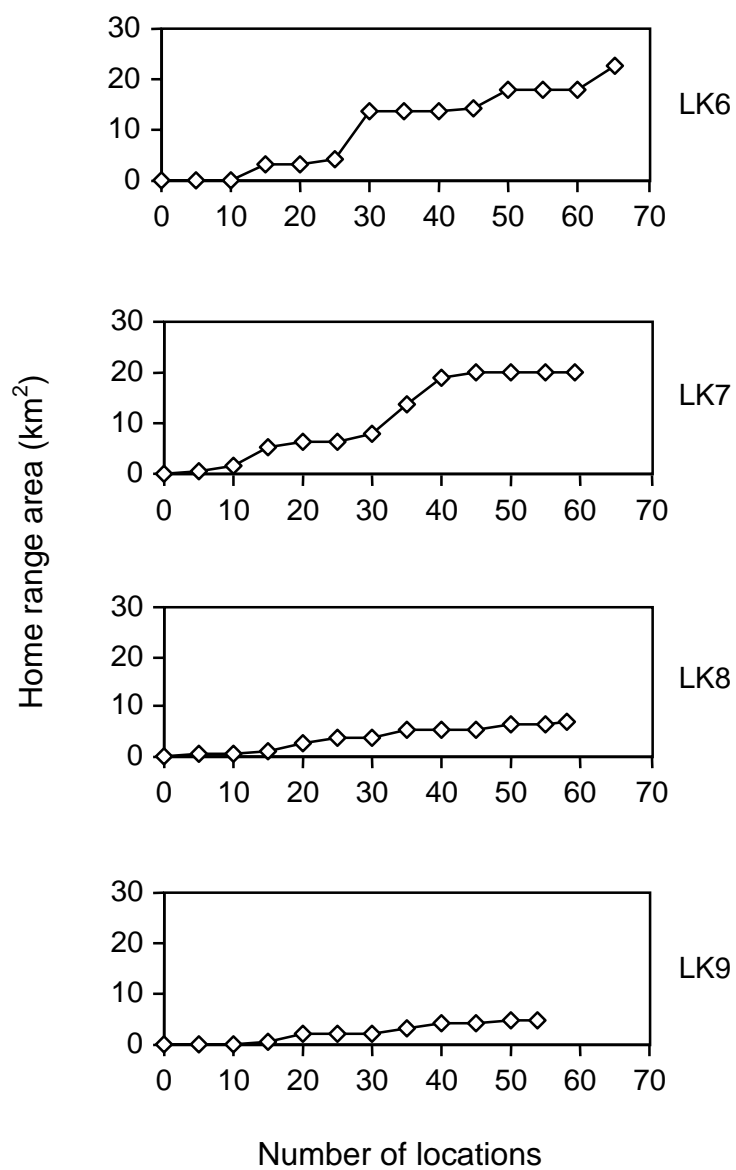


Figure 2-4. continued.

Table 2-3. Mean bearings and vector lengths for telemetered Kemp's ridley turtles during falling and incoming tides. Mean angular deviations given in parentheses.

Turtle ID	Mean bearing incoming tide	No. of fixes	Mean vector length	Mean bearing falling tide	No. of fixes	Mean vector length
LK1	29 (134)	29	0.0639	119 (114)	24	0.1361
LK2	174 (131)	22	0.0724	271 (81)	13	0.3706
LK3	345 (90)	19	0.2885	249 (47)	22	0.7142
LK4	37 (69)	11	0.4881	238 (66)	31	0.5123
LK5	67 (92)	19	0.2790	265 (77)	30	0.4060
LK6	48 (85)	26	0.3308	238 (82)	33	0.3578
LK7	70 (86)	25	0.3245	229 (56)	29	0.6204
LK8	8 (75)	25	0.4268	199 (103)	28	0.1979
LK9	82 (123)	20	0.1004	225 (103)	29	0.1963
Second-order statistics	48 (49)		0.6947	232 (41)		0.7772

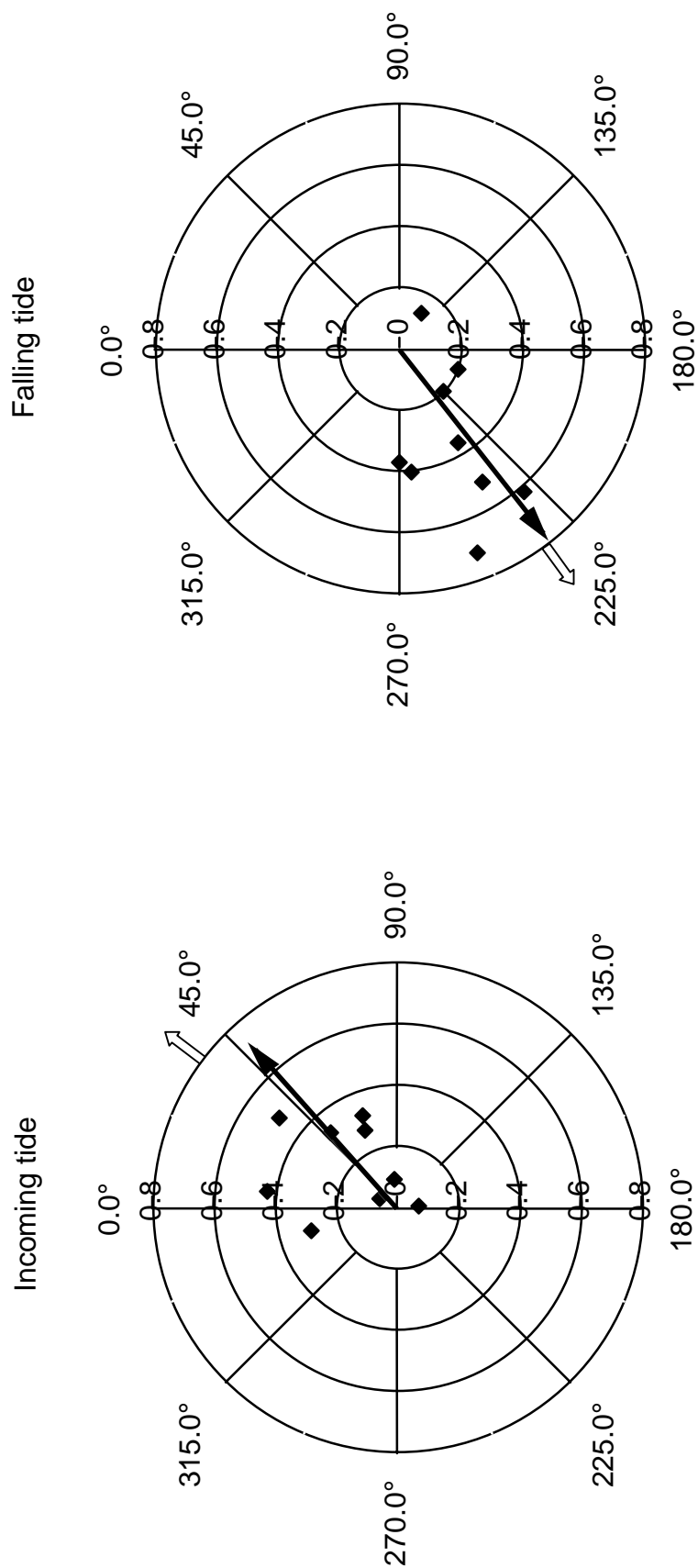


Figure 2-5. Mean bearings and vector lengths by tide state for Kemp's ridley turtles. Black arrows indicate the mean of mean bearings and vector lengths for turtles and white arrows indicate mean tidal bearings for 1995.

mean angular deviations ranged from 56° to 114°. The two datasets with the smallest sample sizes (LK2, falling tide and LK4, incoming tide) exhibited intermediate mean vector lengths, although that of LK4 was also the highest for incoming tides. The distribution of bearings and hourly distances by tide state (Fig. 2-6) indicated three patterns of orientation: undirected movements less than 500 m (LK6 - incoming and LK9 - incoming), movements perpendicular to the direction tidal flow (LK1 - falling and LK8 - falling), and movements corresponding to the direction of the tide (LK3 - falling and LK7 - falling). The first two patterns resulted in decreased mean vector lengths and increased angular deviations.

Rate of Movement

The mean rate of movement (ROM) for all turtles combined was 0.437 ± 0.331 km/hr (range: 0.004 - 1.758 km/hr). There was a significant difference ($\chi^2=34.31$, $p=0.0001$) among the ROM of individual turtles. LK3 had the highest mean ROM (Table 2-4), which was significantly greater than those of LK1, LK8, and LK9. LK3 had the highest recorded ROM, and 18.3% of the observations for LK3 were greater than 1 km/hr. Conversely, LK8 had the lowest mean ROM (Table 2-4), which was significantly lower than the rates of all turtles except LK1 and LK9. LK8 was the smallest turtle tracked in this study (Table 2-1), but mean ROM of turtles was not significantly correlated with carapace length or mass (Spearman corr. coeff.=0.57, $p=0.11$).

Only Kemp's ridley turtles tracked in 1995 had sufficient 24 hr data to test for time interval patterns of ROM. There was a trend for higher mean ROM

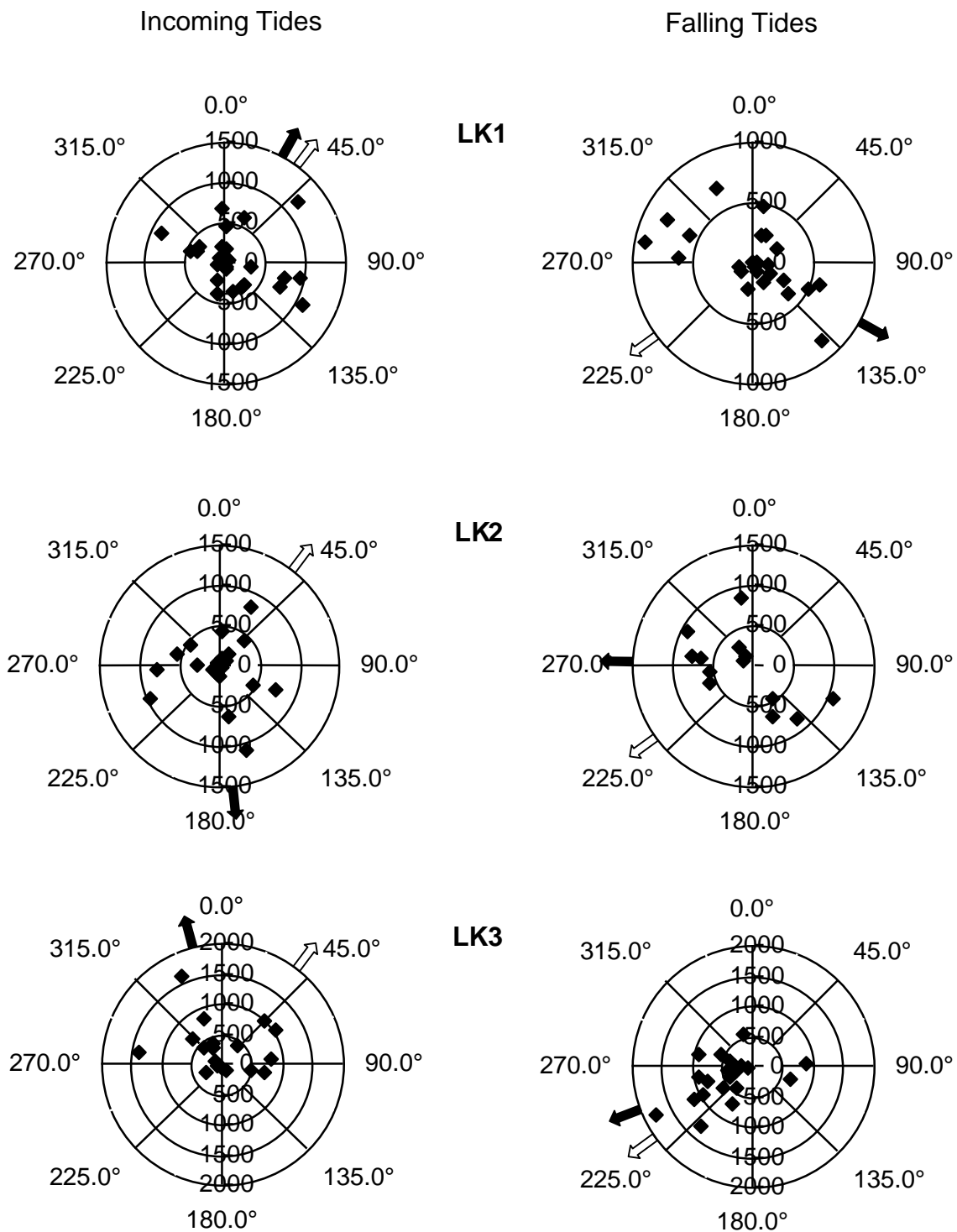


Figure 2-6. Hourly bearings and distances traveled by tide state for Kemp's ridley turtles. Black arrows indicate the mean bearings for turtles and white arrows indicate mean tidal bearings for 1995.

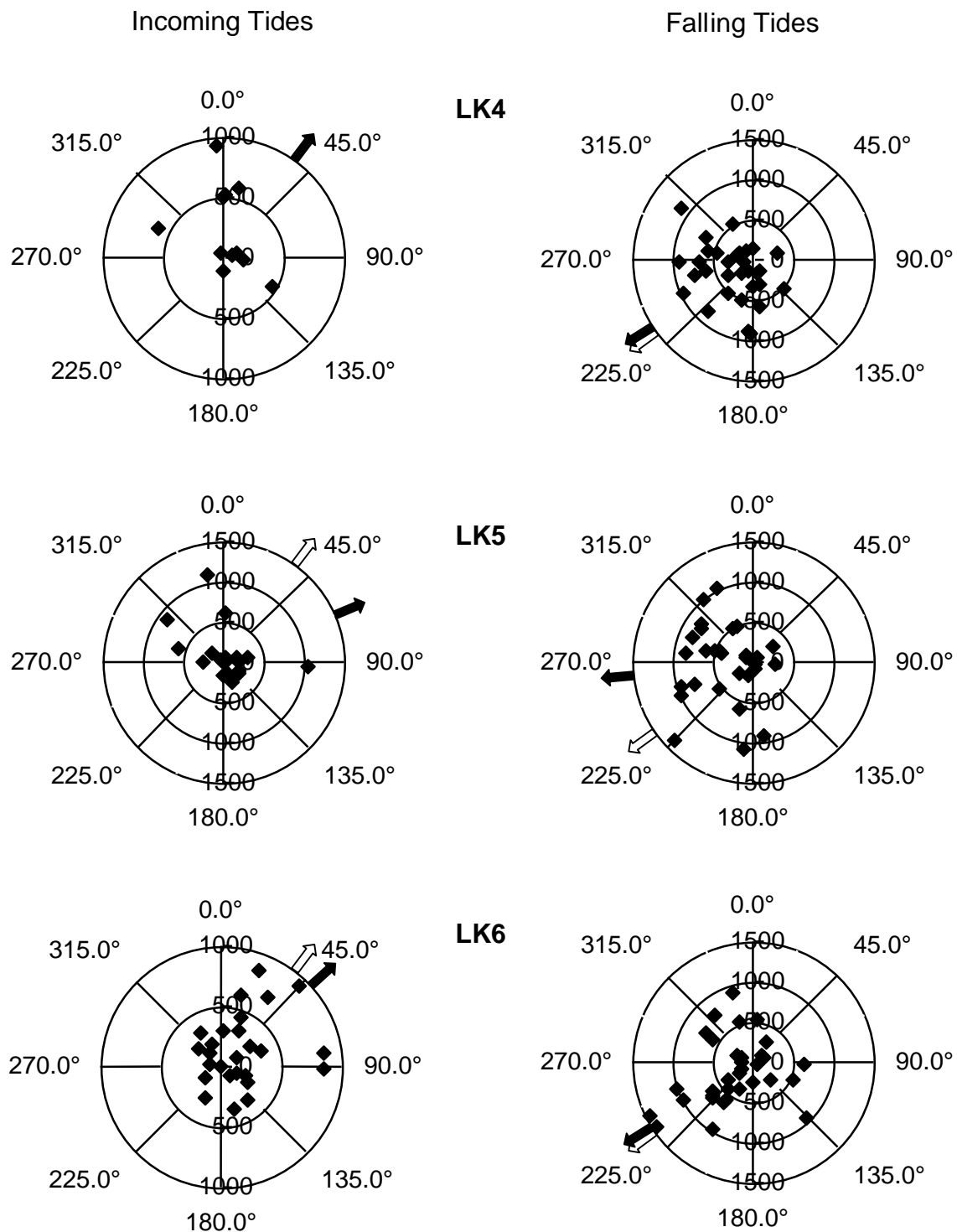


Figure 2-6. continued.

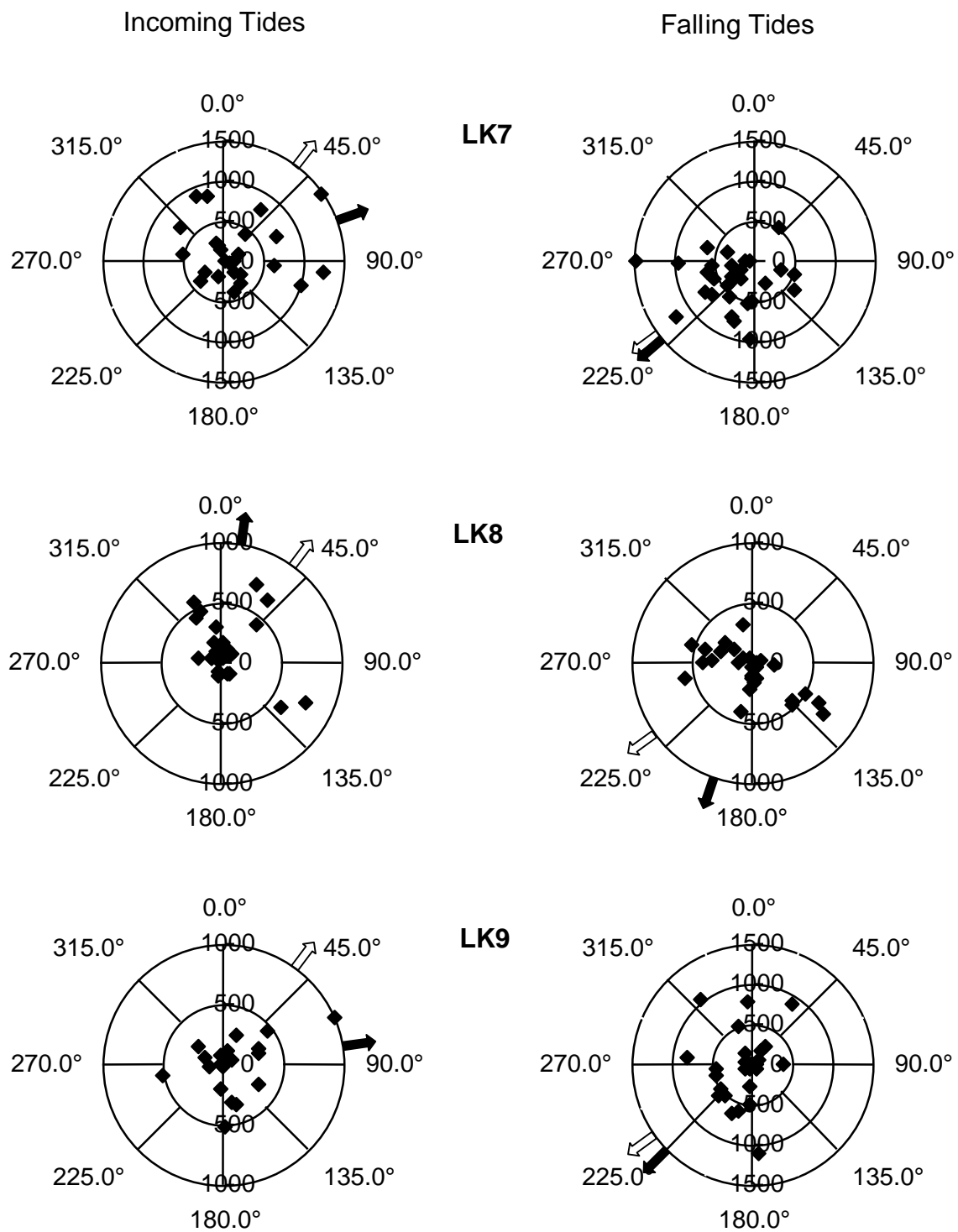


Figure 2-6. continued.

Table 2-4. Mean rate of movement and percent composition of movement rates for Kemp's ridley turtles. Standard deviations are given in parentheses. Means that share the same superscript are not significantly different using the nonparametric multiple comparison procedure.

Turtle ID	Mean rate of movement	Rate of movement (km/hr)			
		< 0.5	0.5-1.0	1.0-1.5	> 1.5
LK1	0.391 ^{a,d} (0.308)	66.1	30.5	3.4	0.0
LK2	0.487 ^{a,b} (0.324)	53.7	41.5	4.9	0.0
LK3	0.600 ^b (0.407)	47.7	34.1	13.7	4.6
LK4	0.441 ^{a,b,c} (0.282)	56.8	40.9	2.3	0.0
LK5	0.478 ^{a,b} (0.366)	58.0	32.0	10.0	0.0
LK6	0.474 ^{a,b} (0.326)	57.6	37.3	5.1	0.0
LK7	0.524 ^b (0.329)	50.0	38.9	11.1	0.0
LK8	0.274 ^d (0.210)	84.9	15.1	0.0	0.0
LK9	0.338 ^{c,d} (0.282)	71.4	28.6	0.0	0.0

during the day for 1995 turtles combined and for individual turtles except LK9 (Table 2-5). However, only the mean ROM of LK7 was significantly greater ($\chi^2=7.87$, $p=0.005$) during the 12 hr day. The mean ROM of this turtle was also significantly different among the 4 level time intervals ($\chi^2=9.53$, $p=0.02$), but the nonparametric multiple comparison procedure failed to indicate which of the levels differed significantly.

Mean ROM was significantly greater on the falling tide (Table 2-6) for all Kemp's ridley turtles combined ($\chi^2=7.11$, $p=0.008$) and turtles tracked in 1995 ($\chi^2=4.11$, $p=0.04$), but was not significantly different for turtles tracked in 1994 ($\chi^2=3.19$, $p=0.07$). There was a trend for higher mean ROM on the falling tide for 6 of the 9 turtles (Table 2-6), but the difference was only significant for LK2 ($\chi^2=5.98$, $p=0.014$) and LK6 ($\chi^2=7.22$, $p=0.007$). Mean ROM of individual turtles differed significantly by tidal state (falling tide: $\chi^2=28.02$, $p=0.0005$; incoming tide: $\chi^2=16.13$, $p=0.041$).

The tide flow data collected in 1995 indicated a trend for higher mean tidal velocities on the incoming tides (Table 2-6), but the difference between tidal states was not significant. For the combined data of 1995, there was a significant positive correlation between tidal speeds and turtle ROM on both falling (Spearman corr. coeff.=0.196, $p=0.02$) and incoming tides (Spearman corr. coeff.=0.232, $p=0.01$). For individual turtles, however, the correlation was only significant for the falling tides of LK7 and the incoming tides of LK8.

Table 2-5. Mean rate of movement (km/hr) for telemetered Kemp's ridley turtles by time of day (W – dawn, D – day, K – dusk, and N - night). A > symbol indicates a significant difference between time intervals using the Kruskal-Wallis test for two levels and the nonparametric multiple comparison procedure for four levels.

Turtle ID	Time of day												
	Two level intervals				Four level intervals								
1995 turtles combined	D	-	N	0.464	D	-	K	-	N	-	W	0.377	0.353
LK5	D	-	N	0.532	D	-	K	-	N	-	W	0.305	-
LK6	D	-	N	0.520	D	-	W	-	K	-	N	0.462	0.422
LK7	D	>	N	0.641	D	-	N	-	K	-	W	0.408	0.370
LK8	D	-	N	0.278	D	-	N	-	W	-	K	0.289	0.141
LK9	N	-	D	0.354	K	-	D	-	N	-	W	0.314	0.261

Table 2-6. Mean rate of movement (km/hr) for Kemp's ridley turtles and mean tidal speed (km/hr) by tidal state. A < symbol indicates a significant difference between tidal states using the Kruskal-Wallis test.

Turtle ID	Mean rate of movement		Mean tidal speed	
	Incoming tide	Falling tide	Incoming tide	Falling tide
All turtles combined	0.394	< 0.476		
1994 turtles combined	0.424	- 0.509		
1995 turtles combined	0.371	< 0.456	0.508	- 0.413
LK1	0.392	- 0.377		
LK2	0.371	< 0.663		
LK3	0.538	- 0.675		
LK4	0.414	- 0.452		
LK5	0.333	- 0.538	0.472	- 0.447
LK6	0.360	< 0.577	0.616	- 0.477
LK7	0.552	- 0.498	0.508	- 0.393
LK8	0.254	- 0.296	0.359	- 0.271
LK9	0.352	- 0.326	0.586	- 0.448

Respiratory Behavior

Field observations indicated that Kemp's ridley turtles exhibited surface durations of 1-2 seconds and submergence durations of 1-2 minutes upon release and continuing for several hours. This pattern was probably in response to the stress of capture and handling, and these data were therefore not included in behavioral analyses. Telemetered turtles exhibited longer surface and submergence durations after the 24-hour acclimation period. Presumably, a 24-hr period of recovery was adequate because this type of respiratory pattern continued through the remainder of the monitoring sessions.

The mean surface duration for all turtles combined was 18 ± 15 seconds (range: 1 - 88 seconds) and the mean submergence duration was 8.4 ± 6.4 minutes (range: 0.2 - 60.0 minutes). However, there were significant differences in the mean surface durations ($\chi^2=368.5$, $p=0.0001$) and submergence durations ($\chi^2=375.1$, $p=0.0001$) among individual turtles ([Table 2-7](#)). The mean surface and submergence durations for LK6 and LK7 were significantly less than those of the other turtles, and 58% of the surface durations for these two turtles were less than 10 seconds ([Fig. 2-7](#)). Furthermore, LK6 and LK7 also exhibited significantly higher mean numbers of surfacings per hour ([Table 2-7](#)). Both of these turtles had injuries to their rear flippers ([Table 2-1](#)), though LK1 had the same type of wounds and did not display a similar respiratory pattern.

Telemetered Kemp's ridley turtles spent 95.7 - 97.0 % of their time submerged ([Table 2-7](#)). Despite the increased frequency of surfacings and shorter respiratory durations, LK7 exhibited the longest surface duration

Table 2-7. Summary of the surface and submergence durations for telemetered Kemp's ridley turtles. Standard deviations are given in parentheses. Means that share the same superscript are not significantly different using the nonparametric multiple comparison procedure.

Turtle ID	Mean number of surfacings per hour	Mean surface duration (sec.)	Mean submergence duration (min.)	Percent time submerged
LK1	5.6 ^{a,c} (1.5)	22.8 ^a (15.1)	10.68 ^{a,b} (6.45)	96.5
LK2	4.9 ^{a,c} (1.9)	17.7 (13.7) ^c	12.15 ^a (8.86)	97.6
LK4	6.3 ^a (3.1)	23.9 ^{a,b} (15.2)	9.05 ^c (5.67)	95.7
LK6	9.6 ^b (4.1)	11.1 (8.8) ^d	5.95 ^d (5.56)	97.0
LK7	9.8 ^b (4.2)	14.8 (13.6) ^e	5.90 ^d (4.48)	95.9
LK8	5.9 ^{a,c} (2.9)	22.3 ^a (14.8)	9.74 ^{b,c} (5.97)	96.3
LK9	5.0 ^c (2.1)	25.9 ^b (16.2)	11.32 ^a (6.28)	96.3

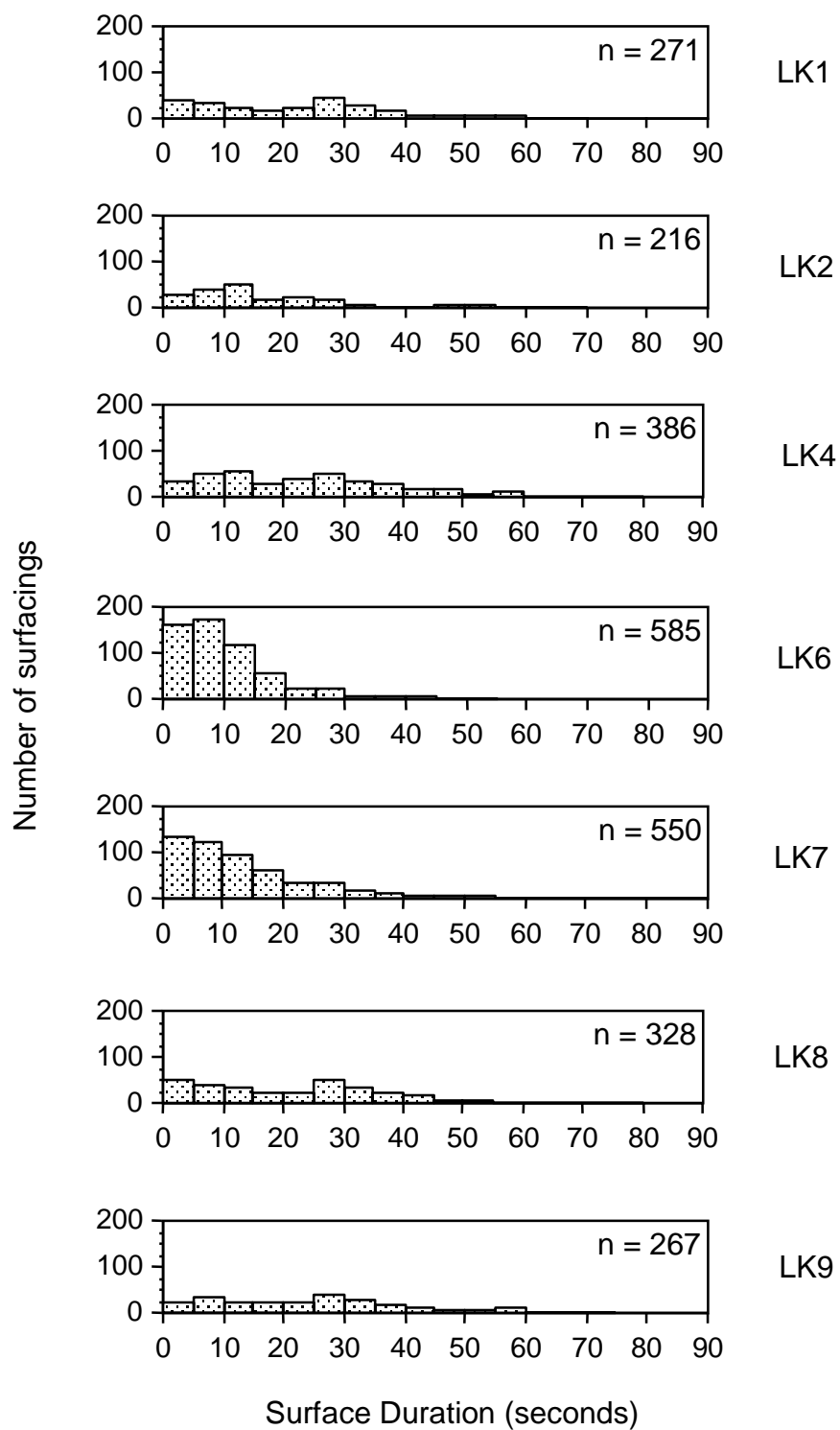


Figure 2-7. Frequency distributions of surfacing duration (10-second intervals) for Kemp's ridley turtles. Numbers indicate total number of surfacings.

(88 seconds) used in the analyses. However, surface durations of 4-8 minutes were recorded for two of the turtles not included in these analyses owing to insufficient data. The longer surface durations recorded for these turtles may be indicative of basking behavior. Non-telemetered Kemp's ridley turtles were observed floating on the surface for extended periods of time, and one such turtle appeared to be resting (motionless with foreflippers tucked laterally) within seagrass flotsam.

Mean surface durations were not significantly different during the two 12 hour time intervals for all turtles combined ([Table 2-8](#)). However, the combined data for each year indicated a significantly longer mean surface duration during the 12-hour day for turtles tracked in 1994 and during the 12-hour night for turtles tracked in 1995. This discrepancy may have resulted from sampling error as 1994 turtles were not systematically monitored for a full 24 hour period. The mean surface duration during the 8-hour night was significantly longer than the 4-hour dusk and dawn for all turtles combined, and was significantly longer than the other four level intervals for turtles tracked in 1995 ([Table 2-8](#)).

Mean submergence durations were significantly longer during the 12-hour night for the combined data of all turtles and turtles tracked during each year ([Table 2-9](#)). For all turtles combined, the mean submergence duration during the 8 hour night was significantly longer than those during the 8-hour day and 4-hour dusk, and the mean submergence duration during the 4-hour dawn was significantly longer than that of the 4-hour dusk. For turtles tracked in 1995, the

Table 2-8. Mean surface durations (nearest second) of Kemp's ridley turtles by time of day (W – dawn, D – day, K – dusk, and N - night). A > symbol indicates a significant difference between time intervals using the Kruskal-Wallis test for two levels and the nonparametric multiple comparison procedure for four levels. Parentheses were used to consolidate significant differences.

Turtle ID	Time of day	
	Two level intervals	Four level intervals
All turtles combined	N19 – D18	(N20 > W17 – K17) – D19
1994 turtles combined	D23 > N19	D19 – W17 – K16 – N14
1995 turtles combined	N18 > D15	N17 > D14 – W13 – K12
LK1	D24 > N19	K27 – D24 – W19 – N19
LK2	D18 – N17	K19 – W19 – D17 – N17
LK4	D24 – N22	W25 – D24 – N24 – K23
LK6	N12 – D10	N14 – K12 – D10 > W7
LK7	N16 – D14	(N18 > K12 – W12) – D15
LK8	N31 > D17	N36 – W28 > D18 – K16
LK9	N27 – D25	(N29 > K21) – D29 – W24

Table 2-9. Mean submergence durations (nearest second) of Kemp's ridley turtles by time of day (W – dawn, D – day, K – dusk, and N - night). A > symbol indicates a significant difference between time intervals using the Kruskal-Wallis test for two levels and the nonparametric multiple comparison procedure for four levels. Parentheses were used to consolidate significant differences.

Turtle ID	Time of day	
	Two level intervals	Four level intervals
All turtles combined	N523 > D494	N545 > D497 – K468 & W520 > K468
1994 turtles combined	N652 > D609	W649 – K642 – N639 – D596
1995 turtles combined	N491 > D410	N521 – W476 > D404 – K394
LK1	D647 – N625	W707 – K699 – D640 – N542
LK2	N739 – D724	N773 – D751 – K712 – W608
LK4	N568 – D539	W611 – N596 – K560 – D524
LK6	N401 > D311	N437 – W367 > K325 – D288
LK7	N362 – D346	N379 – W358 – D351 – K320
LK8	N743 > D493	N793 – W709 > K503 – D476
LK9	N746 > D619	(N817 – D715 > K522) – W675

mean submergence durations during the 8-hour night and 4-hour dawn were significantly longer than those during the 8-hour day and 4-hour dusk.

There were significant correlations between ROM, number of surfacings, and surface and submergence durations for the combined data of all turtles and turtles tracked in 1995, though the significance of these relationships varied for turtles tracked in 1994 and individual turtles ([Table 2-10](#)). Increased ROMs corresponded to increased number of surfacings and decreased surface and submergence durations. The number of surfacings decreased with increasing surface and submergence durations, and increased surface durations corresponded to increased submergence durations.

There were trends for decreasing number of surfacings and surface durations and increasing submergence durations with both increasing carapace length and mass (body size), but the correlations between these variables were not significant. The data of LK6 and LK7 were omitted because of their significantly different respiratory pattern. Subsequently, there were significant positive correlations (Spearman corr. coeff.=0.9, $p=0.04$) between mean submergence duration and body size, and significant negative correlations (Spearman corr. coeff.=-0.9, $p=0.04$) between mean number of surfacings and body size. The largest turtle (LK2; 54.0 cm SCL) exhibited the longest submergence duration (59 minutes). However, submergence durations of 71-84 minutes were recorded for a smaller turtle (36.8 cm SCL) not included in these analyses owing to insufficient data. This turtle was monitored later in the year (late October and early November) than any of the other turtles, during a period

Table 2-10. Spearman correlation analyses of the rate of movement (km/hr), number of surfacings per hour, and mean hourly surface and submergence durations for Kemp's ridley turtles. Number of surfacings and surface/submergence durations were pooled within the time intervals of consecutive locations. P-values are in parentheses and significant correlations are in bold.

Turtle ID		Rate of movement	No. of surfacings	Surface duration
All turtles combined	No. of surfacings	0.3081 (0.0001)		
	Surface duration	-0.2911 (0.0001)	-0.6704 (0.0001)	
	Submergence duration	-0.2911 (0.0001)	-0.9588 (0.0001)	0.6621 (0.0001)
1994 turtles combined	No. of surfacings	0.1438 (0.1155)		
	Surface duration	-0.2809 (0.0018)	-0.3523 (0.0001)	
	Submergence duration	-0.1655 (0.0697)	-0.9197 (0.0001)	0.3329 (0.0002)
1995 turtles combined	No. of surfacings	0.4270 (0.0001)		
	Surface duration	-0.3145 (0.0001)	-0.8079 (0.0001)	
	Submergence duration	-0.3963 (0.0001)	-0.9735 (0.0001)	0.8088 (0.0001)
LK1	No. of surfacings	-0.0345 (0.8329)		
	Surface duration	-0.2047 (0.2051)	-0.2581 (0.1077)	
	Submergence duration	-0.0146 (0.9286)	-0.8456 (0.0001)	0.2197 (0.1731)
LK2	No. of surfacings	0.1676 (0.3145)		
	Surface duration	-0.5295 (0.0006)	-0.1950 (0.2406)	
	Submergence duration	-0.2352 (0.1553)	-0.9269 (0.0001)	0.2818 (0.0866)

Table 2-10. continued.

Turtle ID		Rate of movement	No. of surfacings	Surface duration
LK4	No. of surfacings	0.3156 (0.0393)		
	Surface duration	-0.2030 (0.1918)	-0.7875 (0.0001)	
	Submergence duration	-0.2456 (0.1124)	-0.9449 (0.0001)	0.7708 (0.0001)
LK6	No. of surfacings	0.3633 (0.0047)		
	Surface duration	-0.3190 (0.0138)	-0.6826 (0.0001)	
	Submergence duration	-0.3248 (0.0121)	-0.9736 (0.0001)	0.6287 (0.0001)
LK7	No. of surfacings	0.3903 (0.0035)		
	Surface duration	-0.3004 (0.0273)	-0.7442 (0.0001)	
	Submergence duration	-0.3361 (0.0130)	-0.9765 (0.0001)	0.7330 (0.0001)
LK8	No. of surfacings	0.0808 (0.5651)		
	Surface duration	0.2766 (0.0450)	-0.6421 (0.0001)	
	Submergence duration	0.1652 (0.2372)	-0.9083 (0.0001)	0.6896 (0.0001)
LK9	No. of surfacings	0.5899 (0.0001)		
	Surface duration	-0.3454 (0.0151)	-0.6855 (0.0001)	
	Submergence duration	-0.5495 (0.0001)	-0.8959 (0.0001)	0.7461 (0.0001)

when water temperature typically decreases ([Schmid, 1998](#)). In fact, the longer submergence durations of this smaller turtle were recorded after the passage of a cold front, indicating that the respiratory behavior of Kemp's ridley may also be correlated with seasonal changes in environmental conditions.

Discussion

The Kemp's ridley turtles tracked in the present study typically remained in the vicinity of Corrigan Reef complex and, with the exception of two turtles, the few that left soon returned to areas they had previously occupied. Kemp's ridley turtles utilized relatively confined areas for the duration of the two-week monitoring period and continued for at least 2-3 months. This indicates that turtles may reside within this region for the duration of their seasonal occurrence (April to November; [Schmid, 1998](#)), but long-term tracking (i.e., 6-8 months) is needed to determine the extent of their fidelity within a season. Kemp's ridley turtles also return to Corrigan Reef between seasons as evidenced by the multiannual recaptures of two turtles prior to telemetric monitoring. Between season site fidelity could be investigated by re-instrumenting turtles over consecutive years and comparing their locations each year. However, a much larger sample size would be required owing to the low probability of recapturing a previously telemetered turtle during subsequent years.

Approximately half of the telemetered turtles occupied small and stable home range areas around Corrigan Reef. The home range areas of the other

turtles were larger owing to occasional movements to other areas around the intertidal oyster reef. These excursions may represent turtles searching for more favorable foraging areas, and suggest turtles may periodically expand their ranges to prevent over-exploitation of resources. There was considerable spatial overlap in the home ranges of individual Kemp's ridley turtles, particularly around the southern portion of Corrigan Reef, but the data for each turtle were collected during different time periods. Interactions among turtles (such as competition or territoriality) are not known, and there is no evidence to suggest mutually exclusive ranges. On one occasion, the sonic signals of 2 turtles were received while tracking a third turtle, indicating a close proximity among the turtles given the limited range of the sonic transmitters. However, the locations of all the telemetered animals would have to be collected at the same time in order to determine any possible associations between turtles ([White and Garrott, 1990](#)).

Contrary to [Byles' \(1988\)](#) observations in Chesapeake Bay, the Kemp's ridley turtles in the present study oriented their movements with the direction of the prevailing tide, and increased their rate of movement with increasing tidal velocity. The difference in behavior between studies may represent acclimatization by the turtles to regional differences in tidal conditions. Tidal currents in the Cedar Keys area are relatively strong, especially in the channels that cut through the flats and shoals. As pointed out by [Byles \(1988\)](#), movement with or perpendicular to the tidal flow would be energetically beneficial to a turtle. Comparatively, the tidal flow on the shallow seagrass beds of Chesapeake Bay may not be as strong, resulting in movements by Kemp's ridley turtles that

appear to be non-directed. Non-directed movements have also been reported for Kemp's ridley turtles in the bays of New York Sound ([Standora et al., 1990](#); [Morreale and Standora, 1998](#)), though possible interactions with tidal flow were not presented. Despite significant tidal orientation, Kemp's ridley turtles in the Cedar Keys also exhibited extended (> 2 hours) periods of little or no directed movement regardless of the tidal state. During daylight hours, telemetered turtles were observed surfacing toward the direction of tidal flow when remaining relatively stationary. Apparently, the turtles were swimming against the tidal current while ascending and descending in order to maintain a fixed position. Since turtles were not observed underwater, it is not known whether these stationary periods represent resting at a specific site on the bottom or actively foraging within a confined area. Resting and maintaining a fixed location against the tide would be energetically disadvantageous, while feeding would offset the expenditure of swimming against the current. Therefore, if turtles are optimizing their swimming energetics, it is likely that turtles are foraging during these stationary periods.

There is very little information available on the rate of movement of Kemp's ridley turtles. [Renaud \(1995\)](#) reported an overall mean swimming velocity of 1.0 km/hr, with individual mean velocities of 0.7 to 11.0 km/hr. [Gitschlag \(1996\)](#) recorded a mean rate of movement of 0.82 km/hr for an adult-sized female on the Atlantic coast. However, both of these studies employed satellite telemetry and the authors expressed caution on interpreting these values owing to the lack of accuracy in estimating turtle locations with this telemetric method.

In the present study, the mean rate of movement for Kemp's ridley was 0.44 km/hr with individual mean rates of 0.27 to 0.60 km/hr. The intensive and systematic sonic tracking of turtles, coupled with the locational accuracy of differentially corrected GPS, allowed for precise calculations of travel rates for Kemp's ridley turtles. In addition to differences in spatial accuracy, the time scales between telemetric methodologies are different and may have affected the calculation of overall rates of movement. Nonetheless, the values reported by each study appear consistent with the activities of the turtles. With the exception of a single turtle in the Gulf, the studies using satellite telemetry were tracking Kemp's ridley turtles migrating along the Atlantic coast during fall and winter, when higher rates of movement would be expected. [Gitschlag \(1996\)](#) tracked two other turtles with radio and sonic telemetry that also had high rates of movement during their southerly migration, though the mean values were not reported. The Kemp's ridley turtles tracked in the present study were utilizing summer foraging grounds, when lower rates of movement would be expected, although their rates of movement are likely to increase when they depart the nearshore waters of the Cedar Keys during the fall.

Radio and satellite transmitters have been used to investigate the respiratory behavior of Kemp's ridley turtles, but comparisons among studies are confounded by differences between the telemetric methodologies. The data obtained from satellite transmitters are in terms of submergence patterns and are summarized in 12-hour intervals, whereas the data obtained from radio transmitters are in terms of surfacing patterns and are collected consecutively.

Nonetheless, surface durations can be compared among studies using radio telemetry, and overall submergence behavior can be compared among all studies. The mean surface duration for subadult turtles in the present study is slightly less than that of internesting females, but is 4 and 7 times less than the durations reported for subadults on the Atlantic coast ([Table 2-11](#)). Differences in the attachment of the radio transmitter and the activities of the turtles may explain the discrepancy. [Byles \(1988\)](#) used one-meter lanyards, compared to the approximately 25-36 cm tether lengths used herein, which could have resulted in longer surface duration of the radio transmitters. The turtles tracked by [Gitschlag \(1996\)](#) were actively migrating southward, and the longer surface durations he recorded may have been the result of their travelling in relatively deeper and cooler waters. Despite similarities in percent time submerged, the mean submergence duration in the present study was shorter than that reported by any other investigator ([Table 2-11](#)). No explanation is offered other than a possible combination of the differences between studies (type and attachment of transmitter, depth and temperature of water, and developmental stage and activities of turtles).

Temperature is the main environmental factor influencing the daily activities of terrestrial animals ([Cloudsley-Thompson, 1961](#)). However, daily temperature fluctuations in the aquatic environment are minimized owing to the higher thermal capacity of water. Consequently, the ecological significance of diel patterns in aquatic animals is less clear, though in most cases it is probably related to food acquisition ([Cloudsley-Thompson, 1961](#)). The data available for

Table 2-11. Published sources of surface and submergence durations for Kemp's ridley turtles. Brackets indicate extrapolated values.

Transmitter/attachment	Life history stage ^a	Sample size	Mean surface duration (sec)	Mean submergence duration (min)	% time submerged
Radio/backpack ^b	Inter-nesting females	9	23.7	16.7	[97.6]
Radio/tether ^c	Subadults	2	126.0	12.7	[83.5]
Radio/backpack ^d	Subadults	2	[90.0]	[27.0]	95
Radio/tether ^e	Subadults	16	-	-	1.7 - 95.1
Radio/tether ^f	Subadults	7	18.5	8.4	95.7 - 97.6
Satellite/tether and backpack ^g	Post-nesting females	14	-	18.1	96
Satellite/backpack ^h	Subadults and adult	4	-	33.7	58.9 - 98.5
Satellite/backpack ^d	Adult	1	-	60.2	94

^a As defined by Schmid (1995, 1998).

^b [Mendonça and Pritchard \(1986\)](#).

^c [Bytes \(1988\)](#).

^d [Gitschlag \(1996\)](#).

^e [Morreale and Standora \(1998\)](#).

^f Present study.

^g [Bytes \(1989\)](#).

^h [Renaud \(1995\)](#).

marine turtles provide support for this supposition. Diel activity patterns have been reported for subadult hawksbill ([van Dam and Diez, 1998](#)) and green turtles ([Bjorndal, 1980](#); [Mendonça, 1983](#); [Ogden et al., 1983](#)), but have not been observed in subadult loggerhead turtles ([Byles, 1988](#)) or subadult and post-nesting Kemp's ridley turtles ([Byles, 1988, 1989](#)). The spongivorous hawksbill and herbivorous green turtle fed on sedentary food items that tend to be concentrated in certain areas. Both species forage during daylight and return to resting sites at night. By comparison, the carnivorous loggerhead and Kemp's ridley turtles feed on benthic invertebrates, particularly molluscs by the former ([Dodd, 1988](#)) and crabs by the latter ([Shaver, 1991](#)), and their prey may be widely dispersed, nocturnally active, and relatively mobile. Nightly resting sites were not recorded for either species, indicating that they may be feeding throughout a 24-hour period. Nocturnal feeding has also been hypothesized for inter-nesting leatherback turtles, *Dermochelys coriacea*, as their dive patterns were correlated with the diel migration of the zooplankton that they feed upon ([Eckert et al., 1989](#))

A few telemetric studies of Kemp's ridley turtles have identified the timing of daily activities, but none has suggested reasons for these patterns. Although Kemp's ridley turtles in the present study did not exhibit significant diel patterns of movement, there was a trend for a higher rate of diurnal movement and the significantly longer submergence durations during the night suggest reduced nocturnal movement. Nevertheless, turtles also exhibited periods of little or no movement during all hours of the day and night. Animals engaged in equal

activities throughout a 24-hour period are referred to as nycthemeral, and the adaptive significance of this type of pattern is that it allows for regular bouts of feeding, which in turn should maximize feeding efficiency (Maier and White, 1998). If Kemp's ridley turtles continue to feed at night, they must be using olfactory or auditory cues to find their prey. These methods of prey detection may also be used during the day as the turbid waters surrounding Corrigan Reef limit light penetration and subsequently reduce visibility underwater.

The activity patterns of Kemp's ridley turtles in the Cedar Keys may coincide with the activities of their prey. Stone crabs, *Menippe* spp., and blue crabs, *Callinectes sapidus*, were identified as important food items for Kemp's ridley turtles captured in the vicinity of Corrigan Reef (Schmid, 1998). The stone crab is nocturnally active and capable of sound production by way of stridulating organs on the chela (Powell and Gunter, 1968; Bender, 1971). The possibility of auditory detection of prey could be investigated by capturing turtles and holding them for fecal sample analysis, then exposing turtles that have ingested stone crabs to stridulation and recording their behavior in response to the sound. Telemetric studies of foraging blue crabs indicated that their movements were non-directed with no diel pattern (Hines and Wolcott, 1990; Nye, 1990), although an increase in diurnal movements was noted for premolt crabs (Wolcott and Hines, 1990).

Marine turtles rely on aerobic metabolism during routine activities, and oxygen consumption has been used as an indirect measure of their energy consumption (Wyneken, 1997, and references therein). Captive green (Prange,

1976; [Butler et al., 1984](#)) and loggerhead turtles ([Lutz et al., 1989](#)) demonstrated a three-fold increase in oxygen consumption between resting and moderate swimming speeds, and a corresponding increase in respiratory frequency. Although there are no quantitative data on oxygen consumption by Kemp's ridley turtles, the correlation of movement rates with respiratory activities in the present study is in agreement with the results of swimming performance tests. [Stabenau et al. \(1992\)](#) indicated that the breathing frequency in Kemp's ridley turtles was higher than that of green turtles swimming under similar laboratory conditions ([Butler et al., 1984](#)). Excluding the dissimilarities in turtle sizes and experimental protocols used in each study, this would indicate that there are differences in oxygen consumption, and therefore metabolic rate, between species, and that the metabolic rate of Kemp's ridley turtles is higher than that of green turtles. Inter-specific differences in the breathing frequencies of wild turtles could be investigated by telemetrically monitoring similar-size individuals of both species at the same time and in the same general area, and comparing their patterns of movement and respiratory durations.

Marine turtles are ectothermic and therefore rely on the temperature of the surrounding water to regulate body temperature. This influences their activities as thermoregulation is achieved by moving between contrasting thermal environments ([Lillywhite, 1987](#)). Cooler water temperatures would decrease the metabolic rate of an ectotherm, and, as a consequence, turtles would be expected to have lower number of surfacings and longer inter-respiratory durations. One of the telemetered turtles not included in the present analyses

moved southward to relatively deeper waters after the passage of a November cold front, and subsequently exhibited fewer surfacings with longer submergence durations. As noted in the preceding paragraph, this seasonal influence on activities and respiratory behavior may explain some of the differences among telemetric studies. The question remains as to whether the turtles from the Cedar Keys continue to move southward along the coast as the nearshore water temperature decreases or move to the deeper, warmer waters offshore. Satellite telemetry has been employed to document the seasonal activity patterns of Kemp's ridley turtles along the Atlantic coast ([Standora et al., 1992](#); [Gitschlag, 1996](#); [Morreale and Standora, 1998](#)) and similar methods should be employed to investigate their winter activities in the northeastern Gulf of Mexico.

Energetics also plays an important role in the spatial distribution of marine turtles during their seasonal occurrence in coastal-benthic habitats. [Ogren \(1989\)](#) indicated that smaller turtles have less lung capacity and higher oxygen consumption, which limit their dive duration, although no quantitative data were provided to support this supposition. Nonetheless, he therefore hypothesized that smaller turtles enhance their feeding efficiency by inhabiting shallower waters. Smaller turtles would also be expected to occupy smaller foraging ranges to meet their energy demands, as originally proposed by [McNab \(1963\)](#) and as observed for green turtles by [Mendonça \(1983\)](#). In the present study, there were indications of a relationship between respiratory durations and body size for Kemp's ridley turtles occurring in relatively shallow depths. The results of these analyses, however, represent the upper portion of the size range of subadult

Kemp's ridley turtles found in U.S. coastal waters. Similarly, the lack of relationship between home range area and body size of Kemp's ridley turtles may have been a result of this truncated size range. Telemetric monitoring of smaller size classes, such as those found in the panhandle region of Florida (Ogren, 1989), is needed to provide support for size-specific activity patterns and home range area of subadult Kemp's ridley turtles.

A number of species must be surveyed in order to evaluate McNab's (1963) predictions on energetics and home range size. I therefore collated the available information on home range area and body mass for marine turtles tracked with radio and sonic telemetry on summer foraging grounds (6 studies for 4 species; Fig. 2-8). There was a significant positive correlation (Spearman corr. coeff.=0.56, $p=0.0008$) between the home range area and mass for all the species combined, supporting McNab's (1963) prediction of increasing foraging range with increasing size. Furthermore, the relationship for green turtles was highly significant (Spearman corr. coeff.=0.93, $p=0.0001$) owing to the size-specific foraging behavior of this species. Small green turtles forage on macroalgae growing on reefs and jetties in close proximity to their nightly resting sites (Wershoven and Wershoven, 1989; Guseman and Ehrhart, 1990; Renaud et al., 1995), whereas larger green turtles forage on seagrass beds separated from their nocturnal sites (Bjorndal, 1980; Mendonça, 1983; Ogden et al., 1983). This pattern is supported by studies performed in the southeast U.S. and northeast Caribbean, and does not apply throughout the range of this species. McNab (1963) also identified food types and their relative abundance as

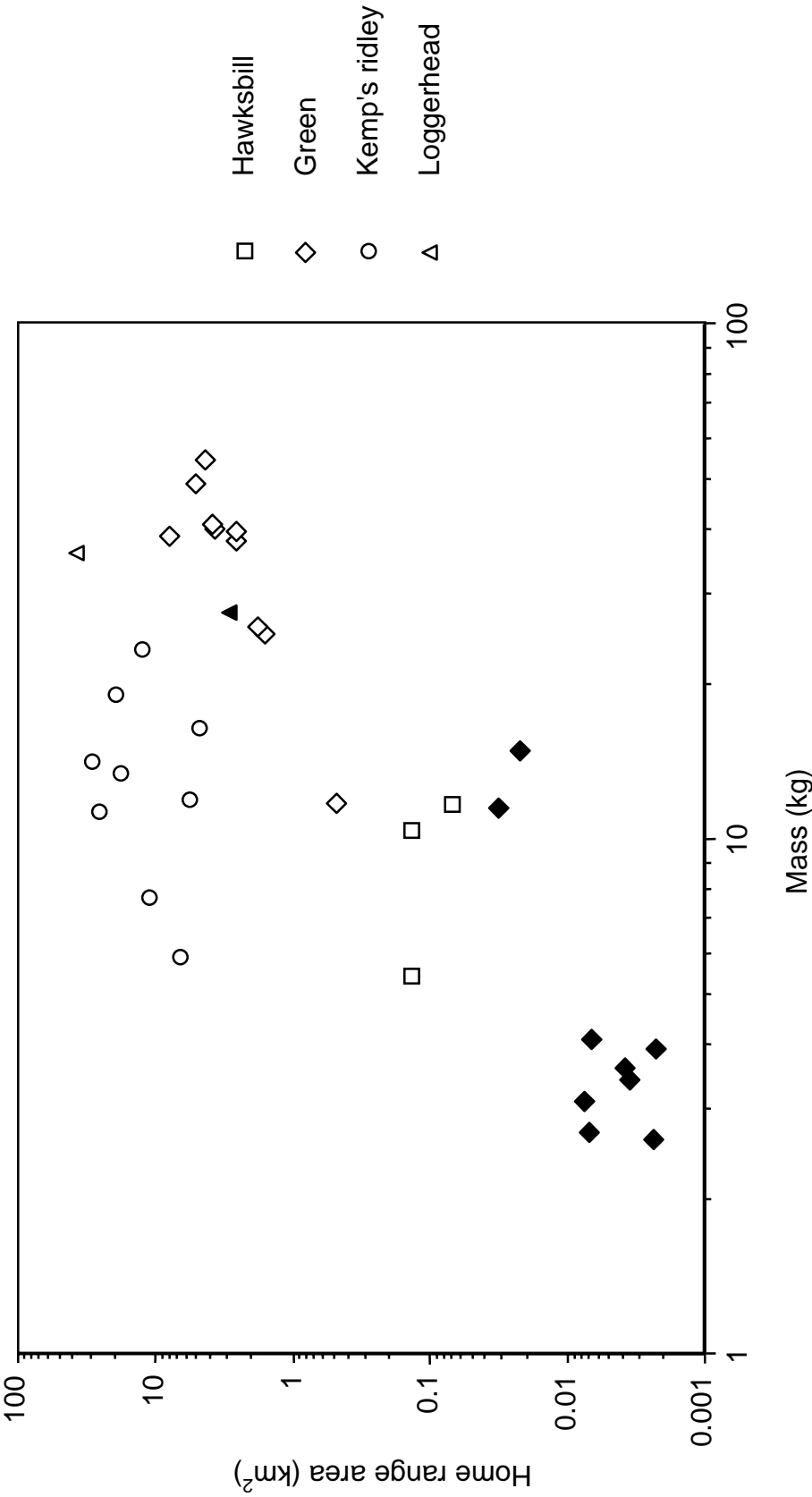


Figure 2-8. Relationship of home range area (km²) and mass (kg) for subadult marine turtles tracked via radio and sonic telemetry. Open squares from [van Dam and Diez \(1998\)](#), open diamonds from [Mendonça \(1983\)](#) and [Ehrhart \(1980\)](#), filled diamonds from [Renaud et al. \(1995\)](#), open circles from present study, open triangle from [Byles \(1988\)](#), and filled triangle from [Epperly et al. \(1995\)](#).

determining factors for the size of a species home range. Accordingly, the marine turtle "croppers" (hawksbill and green turtles) feed on concentrated food sources, and would be expected to have smaller home ranges than the "hunters" (Kemp's ridley and loggerhead turtles). In fact, with the exception of a single loggerhead, the home range areas of the hunters were at least seven times larger than those of the croppers of similar size ([Fig. 2-8](#)).

Admittedly, the data available for home range analyses of marine turtles are scant, and comparisons may be confounded by dissimilar methods among the studies ([Table 2-12](#)). Different techniques of home range estimation and tracking intensity have been shown to produce different estimates of home range size for the same data ([Swihart and Slade, 1985b](#); [White and Garrott, 1990](#)). Only minimum area methods of home range estimation were used in the present analyses, but tracking interval and duration varied among studies. One major disadvantage of minimum area methods is that the size of the home range usually increases as the number of locations increase ([White and Garrott, 1990](#)). Furthermore, use of autocorrelated data results in underestimation of home range size ([Swihart and Slade, 1985b](#)), although intensive sampling during a predefined time frame precludes this effect ([Otis and White, 1999](#)). Nonetheless, the available information for marine turtles concurred with [McNab's \(1963\)](#) predictions, although more data are needed to test the validity of these comparisons. Future telemetric investigations of marine turtles should consider standardizing their methods of data collection and data analysis in order to facilitate comparisons among studies.

Table 2-12. Summary of home range analyses for subadult marine turtles inhabiting summer foraging grounds. CM = *Chelonia mydas*, CC = *Caretta caretta*, EI = *Eretmochelys imbricata*, and LK = *Lepidochelys kemp*.

Source	Species	<i>n</i>	Tracking duration	Tracking intensity	Location estimation	Home range estimation
Mendonça, 1983	CM	9	22-51 days	One location per day; hourly or bihourly when time and weather permitted; and (3) continuous 72 hour tracks	Sonic homing with compass bearing triangulation on nautical charts	Minimum irregular polygon method measured with planimeter
Bytes, 1988	CC	1	51 days	One location per day; more intensive, continuous tracking when time permitted	Sonic homing with LORAN-C or compass bearing triangulation on nautical charts	Minimum irregular polygon method
Renaud et al., 1995	CM	9	44-57 days	Attempted one location daily during all hours of day and night	Sonic homing with locations determined by reference markers on jetty and visual distance estimate; locations >40 m from jetty recorded with GPS when possible	95% minimum convex polygon method modified to exclude non-water areas
Epperly et al., 1995	CC	1	3 days	Total of 17 hrs monitoring between 9:45 and 15:45 with locations every 5 min	Error polygon from sonic signal triangulation; GPS positions for anchored tracking vessels	Area bounded by the extremes of turtle locations measured with Geographic Information System

Table 2-12. continued.

Source	Species	n	Tracking duration	Tracking intensity	Location estimation	Home range estimation
Renaud and Williams, 1997	LK	2	62 & 66 days	Attempted one location every 1-2 days	Visual and sonic homing with GPS; radio triangulation	95% Harmonic Mean method with HOMERANGE program
	CM	1	139 days	between 8:00 and 17:00		
Van Dam and Diez, 1998	EI	3	11-16 days	Locations recorded at 1-4 day intervals; (1) continuous hourly track for each turtle from dawn to dusk	Sonic homing with GPS	Smallest polygon containing all known locations of a turtle
Present study	LK	9	12-66 days	Locations recorded hourly during 4-6 hrs duration, then opportunistically; data collected primarily during day for 4 turtles and systematically during day and night for 5 turtles	Sonic homing with GPS	Minimum convex polygon method with HOMERANGE program

CHAPTER 3

HABITAT ASSOCIATIONS OF KEMP'S RIDLEY TURTLES

Understanding the spatial patterns of resource selection in a heterogeneous environment is an important aspect of animal ecology and wildlife management ([Rosenberg and McKelvey, 1999](#)). Identifying the variables influencing the selection of habitat not only provides an understanding of ecological processes, but also establishes a theoretical basis for habitat management decisions ([Kopp et al., 1998](#)). Optimal Foraging Theory (OFT) predicts that individuals select prey and habitat patches that are most productive to minimize the time and energy spent acquiring food ([MacArthur and Pianka, 1966](#)). Habitat Selection Theory (HST), a branch of OFT, predicts that individuals select particular habitats to enhance their fitness (e.g., survival and reproduction; [Rosenzweig, 1985](#)). Theoretical models of habitat selection incorporate intraspecific ([Fretwell and Lucas, 1970](#)) and interspecific ([Rosenzweig, 1981](#)) interactions as factors influencing habitat selection. Laboratory and field studies correlate the distribution of species relative to habitat attributes (structural characteristics and food availability) in order to identify specific cues associated with the selection of habitat ([Partridge, 1978](#); [Morse, 1985](#)).

Studies of habitat selection in terrestrial wildlife often compare the availability of resources (e.g., food items or habitat types) to those that are

utilized by an animal population. The definition of availability is an essential element in resource selection studies ([McClellan et al., 1998](#)). However, this definition is difficult owing to the subjective criteria used to characterize available resources, the arbitrarily defined boundary of the study area, and the assumption that all resources are available to all individuals. Furthermore, the availability of habitat and forage items depends upon the level of resource selection being considered. [Johnson \(1980\)](#) described a hierarchical ordering of selection processes where first-order selection can be defined as the selection of a species geographical range, second-order selection determines the home range of an individual within the geographic range, third-order selection pertains to the usage of habitat components within the home range, and, if third-order selection determines a foraging site, fourth-order selection refers to the procurement of food items from those available within the site. Analyzing habitat selection at multiple levels minimizes the effects of arbitrarily determining resource availability ([Aebischer et al., 1993](#); [Miller et al., 1999](#)).

Patterns of habitat association result from the summation of individual responses to habitat features ([Wiens, 1985](#)). Radio tracking is customarily employed to provide information on habitat use by individuals in wildlife populations ([White and Garrott, 1990](#)). Habitat types are classified as discrete categories (e.g., soil type and vegetation) and mapped within a defined boundary, and habitat availability is determined from the area of each habitat type relative to the entire study area. Estimates of the proportion of time each telemetered animal utilizes a particular habitat can be obtained by combining the

locational data collected from telemetric monitoring with a map of available habitat. Geographic information systems (GIS) have been used for mapping and analyzing the terrestrial habitats of a number of avian and mammalian species (Ormsby and Lunetta, 1987; Young et al., 1987; Agee et al., 1989; Breininger et al., 1991; Pereira and Itami, 1991; Stone et al., 1997; Staus, 1998; Miller et al., 1999; Smith et al., 1999). Over the past several years, telemetric techniques have been applied to investigate habitat utilization in the marine environment (Rathbun et al., 1990; Wolcott and Hines, 1990; Morrissey, 1991; Szedlmayer, 1997). Furthermore, GIS technology has been identified as an aid to managing the aquatic habitats of the Florida manatee (*Trichechus manatus latirostris*; Reynolds and Haddad, 1990), and recently employed for the analysis of the estuarine habitats utilized by this endangered species (Ambrose, 1998).

Habitat usage by an animal population is selective when the resources are used disproportionately to their availability (Johnson, 1980). Numerous statistical methods are available for comparing use and availability data (Manly et al., 1993; McClean et al., 1998). The choice of a technique is a function of the specific hypotheses to be tested, the types of data used, and the assumptions of the analysis (Aldredge and Ratti, 1986; White and Garrott, 1990). Regardless of the technique employed, the fundamental question is whether an animal population selects some resource types more than others and thus spends more time utilizing these resources than would be expected if all types were used randomly (White and Garrott, 1990). I will refer to comparisons of use-availability data as habitat preference studies, although these investigations are also termed

selectivity (Thomas and Taylor, 1990) or selection studies (Manly et al., 1993; Schooley, 1994). In recent years, compositional analysis (Aitchison, 1986) has been used to examine wildlife habitat preferences, and has been applied to a number of avian species (Aebischer et al., 1993; Carroll et al., 1995; McClean et al., 1998; Staus, 1998; Miller et al., 1999; Smith et al., 1999) and a single reptilian species (Carter et al., 1999).

Wildlife habitat preferences are often described without regard to the availability of habitat and, as such, result in inferences about utilization not preference (Thomas and Taylor, 1990). Studies of marine turtles, particularly the Kemp's ridley turtle, *Lepidochelys kempi*, are an excellent example. Carr (1942) first suggested that this species "preferred" the red mangrove (*Rhizophora mangle*) habitat based on the observations of fishermen in southern Florida. Carr and Caldwell (1956) later noted that Kemp's ridley turtles were also captured near seagrass (*Thalassia testudinum*, turtle grass, and *Syringodium filiforme*, manatee grass) shoals in the west-central Florida turtle fishery. Ogren (1989) identified mud, sand, oyster shell, and turtle grass as bottom types associated with the capture of subadult Kemp's ridley turtles. No "preference" for bottom type was indicated except those corresponding to portunid crab distribution (i.e. shallow seagrass beds and mud bottom bays of coastal marshes). Rudloe et al. (1991) compared the substrates (mud, sand, and seagrass) at the capture sites of subadult turtles in the northeastern Gulf of Mexico and detected "no significant preference" for bottom type. Schmid (1998) suggested that oyster reefs and mud

bottom adjacent to the reefs were being "preferentially utilized" by Kemp's ridley turtles captured near the Cedar Keys, Florida.

[Timko and Kolz \(1982\)](#) first suggested that telemetry could also be used to characterize the habitat preferences of Kemp's ridley turtles, but did not elaborate on the application of the resulting data. [Danton and Prescott \(1988\)](#) observed that a telemetered turtle in Cape Cod Bay remained in the vicinity of a shallow-water shoal composed of extensive eelgrass (*Zostera marina*) flats. [Byles \(1988\)](#) also noted utilization of shoal areas by telemetered Kemp's ridley turtles in Chesapeake Bay, and identified seagrass beds (*Z. marina* and *Ruppia maritima*) as the "preferred" habitat within their foraging ranges. [Renaud and Williams \(1997\)](#) also suggested "preference for specific areas" by turtles tracked in Matagorda Bay. These areas were described as seagrass, although utilization of specific habitats was not identified in this study. In summary, none of the Kemp's ridley turtle investigations to date have quantified the availability of habitat within the respective study areas or the amount of time turtles spent utilizing the habitats in each area.

Estimates of resource availability and use are necessary for identifying coastal foraging habitats that are important to the recovery of the critically endangered Kemp's ridley turtle ([Thompson et al., 1990](#); [U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992](#)). Furthermore, these data are needed to test hypotheses of habitat preferences by this species, and, once habitat utilization and preferences are established, ecological inferences can be made concerning the selection of particular habitat types. The purpose of the

present study is to investigate the habitat associations of Kemp's ridley turtles in the coastal waters of the Cedar Keys, Florida. The objectives are to characterize the benthic habitats available to Kemp's ridley turtles in the Cedar Keys area, to estimate habitat utilization by turtles via telemetric monitoring, and to determine if these turtles exhibit preference for a particular habitat type.

Predictions and Hypotheses

1. The oyster and shell bars of Corrigan Reef and the seagrass shoals of Waccasassa Reefs have been identified as prominent geographic features in the waters east of the Cedar Keys ([Schmid, 1998](#)). I predict the study area will be comprised of a mosaic of these bottom types, and the unvegetated mud and sand flats with rock outcroppings that surround the respective reef complexes.

2. The distribution and movements of Kemp's ridley turtles have been correlated to a variety of benthic habitats ([Carr and Caldwell, 1956](#); [Danton and Prescott, 1988](#); [Byles 1988](#); [Ogren, 1989](#); [Rudloe et al., 1991](#); [Barichivich, 1998](#); [Schmid, 1998](#)). However, none of the investigations to date has quantified habitat utilization or determined whether the turtles prefer a particular habitat type given the availability of all other types. I will test the null hypothesis that Kemp's ridley turtles are randomly utilizing benthic habitats in proportion to their availability within the Cedar Keys study area and the foraging ranges of individual turtles.

3. Subadult Kemp's ridley turtles typically inhabit shallow estuaries when foraging in U.S. coastal waters. Telemetric studies have indicated that Kemp's

ridley turtles utilize waters less than 5 m in Chesapeake Bay (Byles, 1988) and less than 8 m in Long Island Sound (Standora et al., 1990), but there have been no investigations of depth preferences by this species. In the northeastern Gulf of Mexico, Kemp's ridley turtles were captured in waters less than 6 m deep, and all but one of the turtles < 25 cm carapace length were caught in waters less than 1 m deep, prompting Ogren (1989) to suggest that subadult turtles exhibit a size-specific depth utilization. I will test the null hypothesis that Kemp's ridley turtles are randomly utilizing depths in proportion to their availability within the Cedar Keys study area and the foraging ranges of individual turtles. Furthermore, I will test the null hypothesis that the depths utilized by Kemp's ridley turtles do not increase with increasing carapace length.

Materials and Methods

Data Collection

Turtle capture and telemetry

Turtles were collected on the west coast of Florida, approximately 5 km east of the Cedar Keys (Fig. 3-1). A detailed description of the capture sites and methods is provided in Chapter 2 and by Schmid (1998). After measuring and tagging, turtles were instrumented with a sonic transmitter (model CHP-87-L; Sonotronics, Tucson, AZ) and a tethered, buoyant radio transmitter (MOD-050 transmitter with a TA-7 antenna; Telonics, Mesa, AZ). Telemetered turtles were

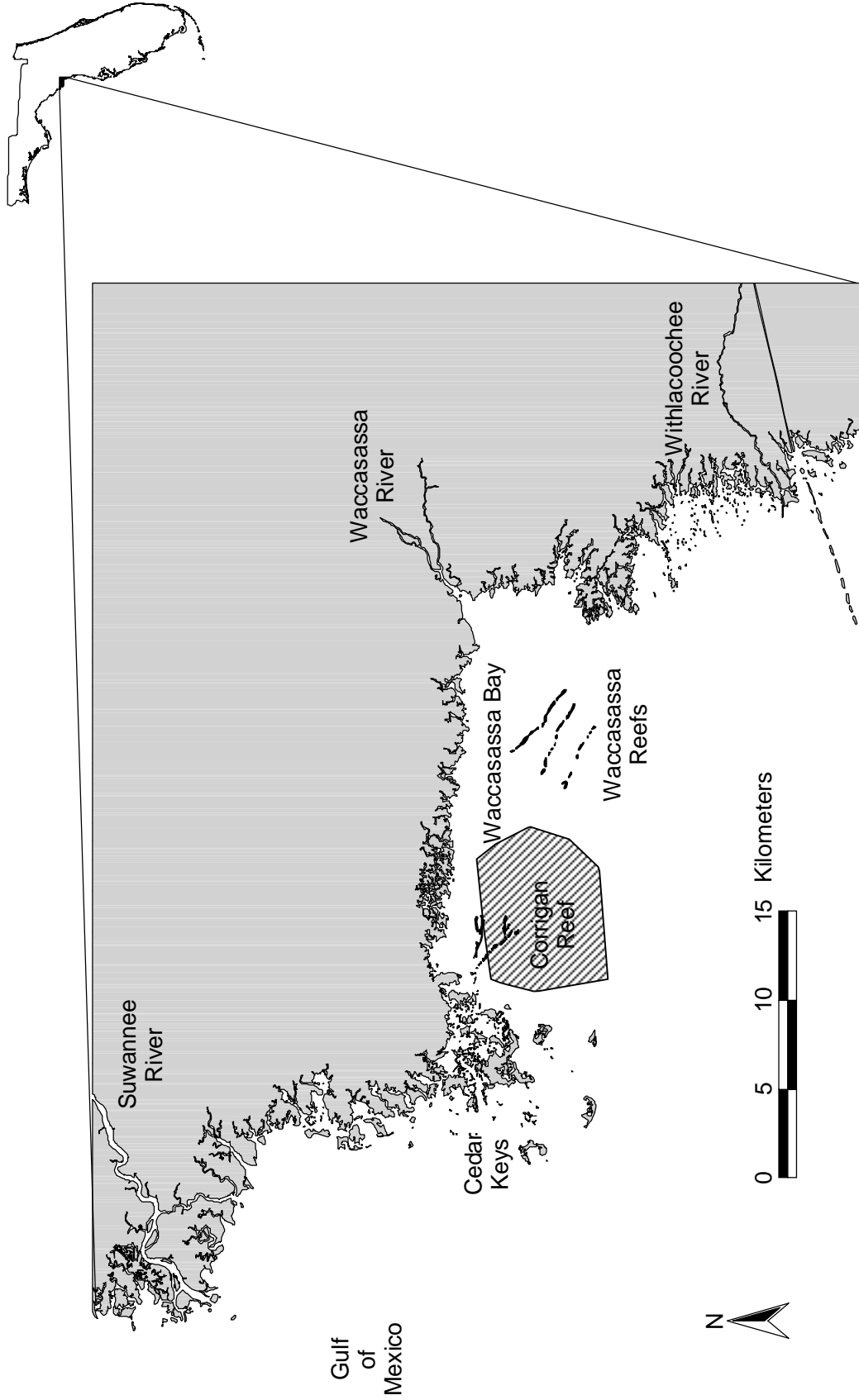


Figure 3-1. Map of west-central Florida showing the study area (crosshatched polygon) for Kemp's ridley turtle habitat analyses.

released in the area of capture, and tracking began after a 24-hour acclimation period. Hourly turtle locations were collected by maneuvering the tracking vessel within 10 - 20 m of the turtle and recording the location of the tracking vessel with differentially corrected Global Positioning System (DGPS; NAV 5000DX with software upgraded to NAV 5000DLX, Magellan Systems Corp., San Dimas, CA). Accuracy of the DGPS locational estimate was approximately 5 m as determined from the variability associated with a fixed position of the vessel. Distances to telemetered turtles were estimated from the strength of the sonic signal at half gain on a N30A5B directional hydrophone and receiver (Dukane Corp., St. Charles, IL).

Tracking was conducted opportunistically in 1994, and most data were collected during the day. In 1995, turtles were systematically monitored for 4 tracking intervals of approximately 12 hours each, so that observations were collected each hour over two 24-hour cycles. At least 24 hours elapsed before initiating the second tracking interval, at least 48 hours elapsed before initiating the third interval, and at least 24 hours elapsed before initiating the fourth interval. After the intensive tracking period, turtles were located opportunistically to establish their presence in the study area. Intensive tracking efforts were abandoned if a turtle traveled more than 6 km from South Bar Light located south of Corrigan Reef.

Study area delineation

A composite home range of turtles tracked in 1995 was used to delineate the study area ([Porter and Church, 1987](#)). The computer program HOME RANGE ([Ackerman et al., 1990](#)) was used to calculate the coordinates of a minimum convex polygon (MCP). East-west transects spaced at 100 m intervals were overlaid on the study area polygon. Sampling sites were located at 100 m intervals along each transect. Transects with turtle locations at or near the endpoints were extended an additional 100 m. The sample site coordinates were uploaded from a personal computer to the GPS. Display graphics of the GPS were used to navigate the transects (routes) and sampling sites (waypoints) during the benthic sample collections of 1996.

Habitat characterization

Benthic substrates and associated biological assemblages were used to classify habitats within the study area. Sediment characteristics were adopted from [Lambe and Whitman \(1969\)](#), and biotic characteristics were adopted from [Continental Shelf Associates, Inc. and Martel Laboratories Inc. \(1985\)](#) and [Wolfe \(1990\)](#). Characterization of each bottom type is outlined below:

Benthic Substrates:

- a) shell - mollusc shell fragments retained by a No. 4 sieve (4.76 mm).

- b) sand - shell and rock particles and coralline algae sediments passing through a No. 4 sieve and retained on a No. 200 sieve (0.074 mm).
- c) mud - silt and clay particles passing through a No. 200 sieve.
- d) rock - outcrops of limestone bedrock.

Biological Assemblages:

- a) seagrasses - *Thalassia testudinum* (turtle grass),
Syringodium filiforme (manatee grass),
Halodule wrightii (shoalgrass), and
Halophila englemanni.
- b) green macroalgae - *Caulerpa prolifera*, *C. mexicana*, *C. sertularoides*, *C. ashmeadii*, *C. cupressoides*, *Udotea conculata*,
Acetabularia crenulata, and *Halimeda incrassata*
- c) red macroalgae - *Gracilaria* spp.
- d) brown macroalgae- *Padina* sp.
- e) live bottom - sessile invertebrates of the phyla
Porifera (sponges), Cnidaria
(gorgonians), Bryozoa (bryozoans), and
Chordata (tunicates).

A grab sampler was deployed shipboard to collect substrate at each sample site. A wet-sieving method (adopted from [ASTM, 1993](#)) was used to sort the benthic substrates in the field. Approximately 125 ml of wet sediment was rinsed through No. 4 and No. 200 sieves with seawater pumped by a 360 gph submersible bilge pump. Percent composition of shell, sand, and mud was estimated from visual inspection of the portions remaining within the sieves. The presence of rock was determined with a sounding pole. Depth at each sample site was recorded in 10 cm increments using a sounding line.

Data Analysis

Habitat mapping

The computer program HOME RANGE ([Ackerman et al., 1990](#)) was used to calculate MCP coordinates from the locations of each turtle. Turtles with > 40 locations were used for the analyses of habitat associations ([Table 3-1](#)). Locational data were omitted for a turtle positioned in clam leases (LK5, n=3), because benthic samples could not be collected in these areas, and for turtles tracked outside of the study area polygon in 1994 (LK2, n=5; LK3, n=9; and LK4, n=10). Turtle locations and home range coordinates were converted to point and polygon themes, respectively, with ArcView version 3.0 (Environmental Systems Research Institute, Redlands, CA) GIS software. Home ranges were buffered 100 m to encompass turtle locations on the corners and perimeter of the polygons.

Table 3-1. Summary of Kemp's ridley turtles used in habitat analyses at the Cedar Keys, Florida.

Tag code	Turtle ID	Carapace length (cm)	Mass (kg)	Contact duration	Number of locations	Convex polygon (km ²)
1994 season						
PPY 168 – 169 ^a	LK1	43.4	11.8	5/30 - 7/15	69	5.82
PPY 172 – 173 ^b	LK2	54.0	23.1	6/19 - 7/01	47	12.89
PPY 175 – 176 ^c	LK3	46.2	14.1	7/09 - 7/26	50	29.51
PPY 177 – 178 ^d	LK4	36.6	7.7	8/01 - 8/27	53	11.40
1995 season						
PPY 183 – 184	LK5	41.9	11.3	5/04 - 6/15	57	25.85
PPY 185 – 186 ^e	LK6	46.0	13.4	5/22 - 7/27	65	17.97
PPY 191 – 192 ^f	LK7	49.9	19.0	6/19 - 7/24	59	19.74
PPY 195 – 196	LK8	34.7	5.9	7/14 - 9/22	58	6.66
PPY 197 – 198 ^g	LK9	49.3	16.3	8/05 - 8/19	54	4.92

^a Originally tagged 10/3/91, recaptured 9/20/92, and recaptured 5/2/94. Missing distal ends of rear flippers.

^b Notches in marginal scutes (resembling mating scars).

^c Large notch in left marginal scutes.

^d Large notch in left marginal scutes.

^e Notches in right marginal and left postcentral scutes. Missing distal end of right rear flipper.

^f Large notch in right marginal scutes. Severing wound to right rear flipper.

^g Originally tagged 1991 (marginal mark), recaptured 9/19/93, and recaptured 8/5/95. Notches in right marginal and postcentral scutes.

A GIS base map of the benthic substrates was generated from the habitat database. The substrate at each sample site was determined from the highest percentage of mud, sand, or shell and, in the absence of these strata, the presence of rock. Habitat maps were constructed by overlaying biological assemblages on the substrate base map. Assemblages were layered hierarchically with the least abundant layer above the more abundant layers, such that assemblages on the top masked those below. Habitat maps were converted from vector (point) to raster (grid; 100 x 100 m cells) format with the ArcView Spatial Analyst extension. The coastline was mapped using digital files of National Oceanic and Atmospheric Administration (NOAA) nautical charts ([Rohmann, 1998](#)).

Water depth at each sampling site was standardized to mean lower low water (MLLW) using hourly water level observations recorded at the Cedar Key tidal station (National Ocean Service, National Oceanic and Atmospheric Administration, Silver Springs, MD). Water levels between successive hourly observations were extrapolated at 6 minute intervals. Depth at a given sample site was calculated from the recorded sounding minus the corresponding water level at 6 minute intervals. A raster map of depths within the study area was generated with ArcView.

Habitat preference

[Aebischer et al. \(1993\)](#) recommend compositional analysis ([Aitchison, 1986](#)) of habitat preferences at two levels: 1) habitat utilization within the home

range of each turtle compared to the habitat availability in the overall study area, and 2) habitat utilization at each turtle's locations compared to the habitat availability in its home range area. These correspond to [Johnson's \(1980\)](#) second-order and third-order levels of habitat selection, respectively. Habitat availability was determined from the proportion of each habitat type within the home range of each turtle or the composite home range of turtles tracked in 1995. Habitat utilization by turtles was estimated from the proportion of turtle locations within each habitat or the proportion of each habitat within the home range of each turtle. Null proportions were replaced with 0.0001 as suggested by [Aebischer et al. \(1993\)](#).

Utilization and availability data were analyzed using a [SAS \(1989\)](#) command file created by [Ott and Hovey \(1997\)](#). Multivariate analysis of variance (MANOVA) was used to test whether differences in log-transformed use and availability proportions were significantly different from zero ($P < 0.05$). Significance levels were determined from randomization due to the potential nonnormality of the multivariate data ([Aebischer et al., 1993](#); [Carroll et al., 1995](#)). In the event of significant nonrandom use, all possible pairs of habitat types were compared and ranked in order of utilization. The pattern of t values in the ranking matrix was used to assess significant differences ($P < 0.05$) in the utilization of habitat types. Analyses of habitat preference by turtles were applied to the benthic substrate basemap and all possible combinations of biological assemblages. Percent compositions of the habitat types used in each compositional analysis are provided in [Appendices A – C](#). Depth preferences by

turtles were also investigated using compositional analysis. Percent compositions of depth at 0.5 m intervals are provided in [Appendix D](#).

[Aebischer et al. \(1993\)](#) recommended sample sizes above 10, preferably above 30, to adequately represent an animal population when conducting compositional analyses of habitats. The number of individuals must be greater than the number of habitat types to show a significant difference using MANOVA ([Aebischer et al., 1993](#); [Miller et al., 1999](#)). Nine turtles would be the absolute minimum for the analyses of habitat and depth preference in the present study since the maximum number of habitat types or depth intervals was eight. While this sample size would be considered low for compositional analysis, it is relatively large when compared to other investigations of Kemp's ridley turtles employing radio and sonic telemetry. [Morreale and Standora \(1998\)](#) tracked a total of 26 Kemp's ridley turtles, 4 - 10 turtles per year, over a four year period in one of the most comprehensive behavioral studies of this species to date. Tracking the movements of an animal that spends most of its time underwater is labor intensive and costly, thus limiting the sample size and the duration of data collection.

Major assumptions of the analyses of habitat preference were that the bottom types sampled in 1996 were representative of those utilized by turtles in 1994 and 1995, and that the aggregation of turtles in the study area utilized the same habitats types both years. Sample sizes were inadequate to test for differences in habitat utilization between years. Physical processes that may have altered the bottom composition of the study area include tidal currents and

waves generated by storms (Brooks and Doyle, 1998). No major hurricanes or winter storms occurred in this region during the three-year period of data collection. Furthermore, the Cedar Keys archipelago and the shoals extending approximately 5 km east-southeast of Snake Key are an effective barrier to any wave action produced in the Gulf of Mexico. Tidal flow is considerable in this region, but it is not known to what extent it may have altered the benthic habitat over the course of the study. McRae (1950) noted the occurrence of lumps of coal in his dredge samples from the northwestern region of the present study area and indicated that very little deposition had occurred as it had been many years since the use of coal for steamships in commercial shipping at the Cedar Keys.

Results

Habitat Availability

The composite of turtle locations collected during the 1995 season produced a 46.44 km² study area polygon with a total of 4,808 sample sites (Figs. 3-1 and 3-2). Of this total, 81.0% ($n=3,893$) of the sites were classified as sand, 14.2% ($n=684$) as rock, 2.1% ($n=103$) as shell, 2.0% ($n=94$) as mud, and 0.7% ($n=34$) as clam aquaculture leases (Fig. 3-2a). Furthermore, the presence of rock was recorded at 53.0% ($n=2,063$) of the sites classified as sand, 18.1% ($n=17$) of the sites classified as mud, and 10.7% ($n=11$) of the sites classified as

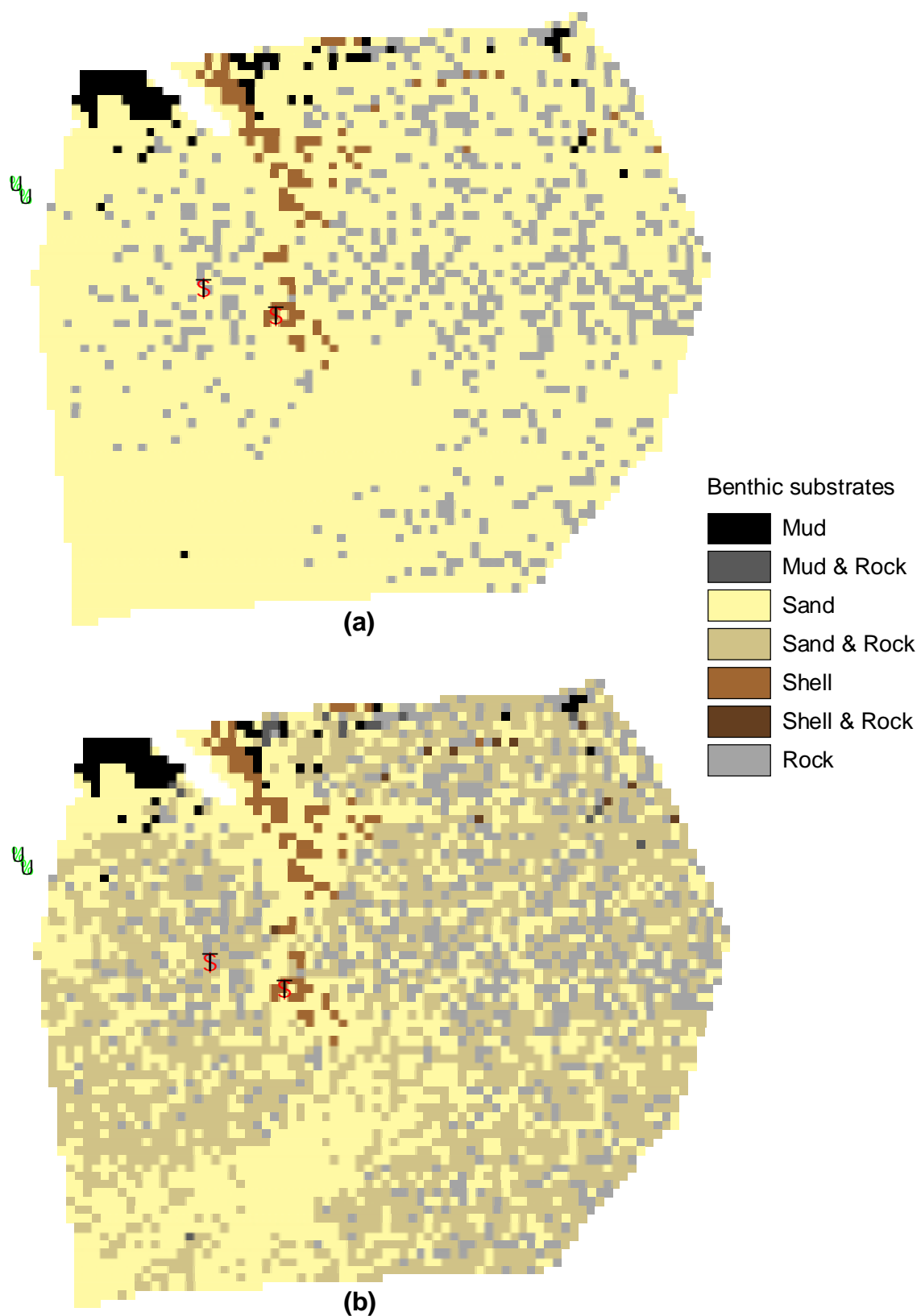


Figure 3-2. Habitat maps of (a) primary benthic substrates and (b) substrates with rock within the study area.

shell ([Fig 3-2b](#)). For the sites classified as shell, 71.8% ($n=74$) were comprised of oyster, *Crassostrea virginica*, most of which were shells of dead individuals. The northwestern region of the study area was comprised of mud bottom and clam aquaculture sites, the north-central region was comprised of shell, and the remainder of the area was comprised of sand with rock outcroppings. Clam lease sites were not included in habitat analyses as no data were collected for these locations.

Green macroalgae species were collected at 27.4% ($n=1,306$) of the sample sites, seagrasses at 17.8% ($n=850$), live bottom at 9.0% ($n=431$), red macroalgae at 7.3% ($n=346$), and brown macroalgae at 0.3% ($n=14$). The principal components of the seagrass assemblage were *Halodule wrightii* (61%; [Table 3-2](#)) and *Halophila englemanni* (32%). The principal components of the green macroalgae assemblage were *Caulerpa prolifera* (53%) and *Udotea congulata* (21%). Red macroalgae were difficult to identify in the field, but the assemblage was composed primarily of *Gracilaria* spp. The seagrass species were predominantly collected on sand substrate, whereas higher percentages of algae species were collected on rock ([Table 3-2](#)). Seagrasses and green macroalgae were distributed in the southern and eastern regions of the study area ([Fig. 3-3](#)). Sponge (64%) and gorgonians (22%) were the principal components of the live bottom assemblage. Live bottom components were collected on rock or sand with rock outcroppings ([Table 3-2](#)) distributed throughout the study area ([Fig. 3-3](#)). The brown algae assemblage was composed of a single species of *Padina* and was not included in the analyses

Table 3-2. Percent composition of primary substrates for the biological assemblages and their species components.

Biological assemblage	Components	Percent of assemblage	Percent substrate composition				Percent of sand sites with rock
			Mud	Sand	Shell	Rock	
Seagrasses	<i>Halodule wrightii</i>	61.29	0.12	98.94	0.24	0.71	42.45
	<i>Halophila englemanni</i>	31.81	0.15	99.09	0.30	0.46	39.17
	<i>Syringodium filiforme</i>	5.50	0.00	99.12	0.00	0.88	50.59
	<i>Thalassia testudinum</i>	1.40	0.00	100.00	0.00	0.00	27.12
Green Algae			0.00	100.00	0.00	0.00	6.67
	<i>Caulerpa prolifera</i>	53.17	0.15	84.53	0.69	14.62	59.69
	<i>C. mexicana</i>	12.84	0.11	82.03	0.99	16.87	57.39
	<i>C. sertularoides</i>	0.35	0.00	84.47	0.00	15.53	70.27
	<i>C. ashmeadii</i>	5.51	0.00	100.00	0.00	0.00	66.67
	<i>C. cupressoides</i>	2.46	0.00	96.81	0.00	3.19	55.32
	<i>Udotea conculata</i>	20.98	0.00	80.95	0.00	19.05	70.59
	<i>Acetabularia crenulata</i>	1.29	0.28	90.78	0.00	8.94	51.08
Red Algae	<i>Halimeda incrassata</i>	3.40	4.55	86.36	0.00	9.9	89.47
			0.00	82.76	0.00	17.24	91.67
Brown Algae	<i>Gracilaria</i> spp.	97.98	0.00	48.97	0.88	50.15	70.59
Live Bottom	<i>Padina</i> sp.	100.00	0.00	42.86	0.00	57.14	83.33
	Sponges	63.82	0.00	38.05	3.02	58.93	82.93
	Gorgonians	22.37	0.00	35.39	4.12	60.48	80.58
	Bryozoans	7.89	0.00	42.16	0.00	57.84	97.67
	Tunicates	5.92	0.00	55.56	2.78	41.67	70.00
			0.00	25.93	3.70	70.37	85.71

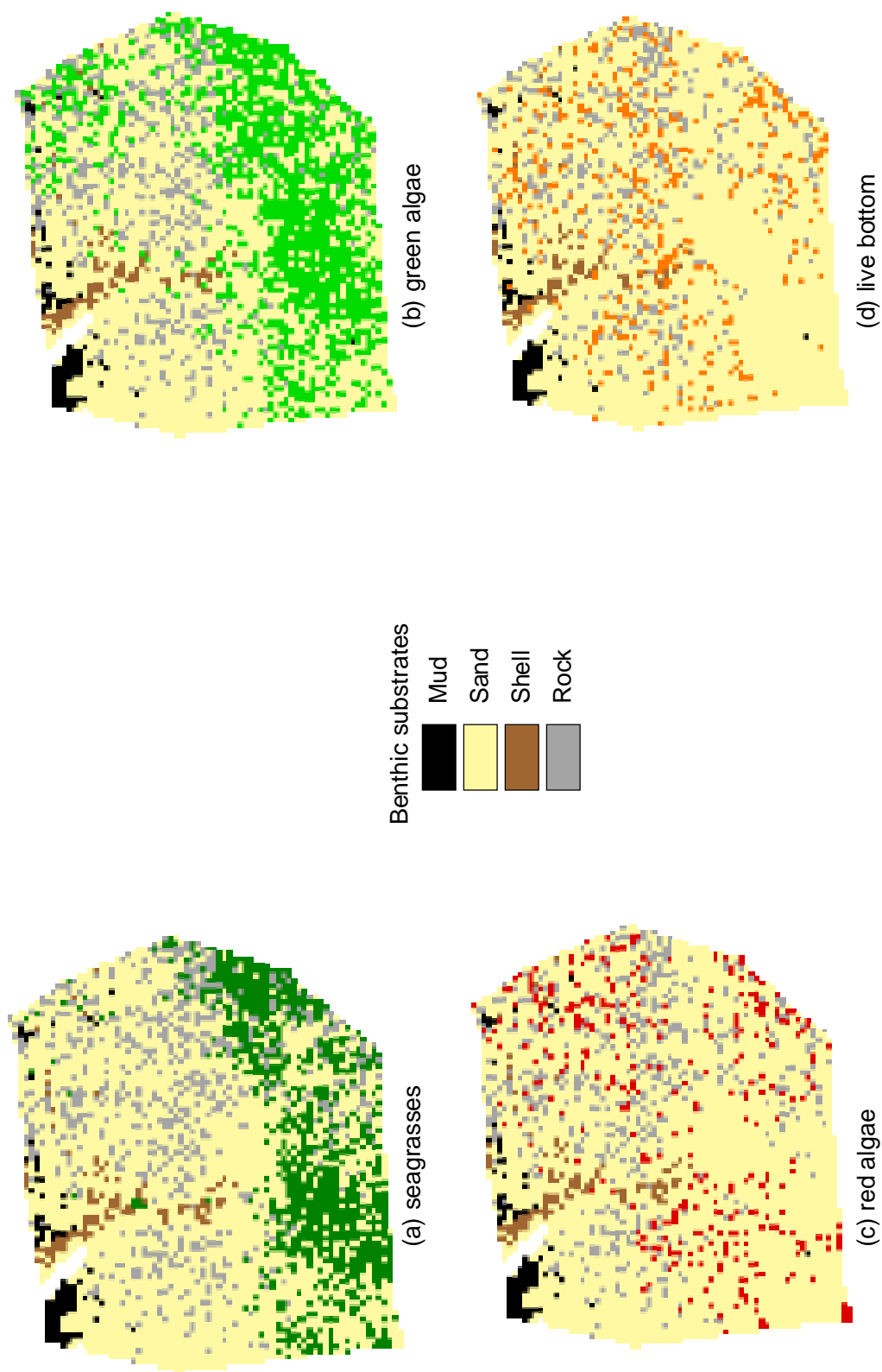


Figure 3-3. Habitat maps of (a) seagrasses, (b) green algae, (c) red algae, and (d) live bottom within the study area.

owing to its low frequency of occurrence. The availability of biological assemblages associated with rock substrate was probably underestimated given the preponderance of outcroppings in sites classified as sand (Table 3-2).

Habitat Utilization

The benthic substrate with the highest mean proportion of utilization was sand ($79.6 \pm 5.3\%$ for home ranges and $78.5 \pm 6.0\%$ for locations; Fig. 3-4), followed by rock ($16.6 \pm 4.2\%$ and $18.7 \pm 3.7\%$). However, the presence of rock outcroppings was recorded in a high proportion of the utilized sand bottom ($59.0 \pm 9.0\%$ and $54.2 \pm 11.0\%$). Green macroalgae had the highest mean proportion of utilization for biological assemblages ($24.0 \pm 20.9\%$ and $22.8 \pm 22.4\%$; Fig. 3-4), followed by seagrasses ($13.0 \pm 16.9\%$ and $10.2 \pm 13.2\%$), and live bottom ($10.3 \pm 1.8\%$ and $12.1 \pm 3.6\%$). There was a high degree of variability in the utilization of green macroalgae and seagrasses by individual turtles. The utilized habitat of LK1, LK8, and LK9 was less than 1% seagrass and 10% green macroalgae, whereas the utilized habitat of LK4 and LK6 was greater than 30% seagrass and 50% green macroalgae.

Habitat Preference

Rock had the highest ranking for combinations of primary substrates (Table 3-3). With the addition of individual biological assemblages, rock was ranked highest in all significant second order analyses, and mud was ranked

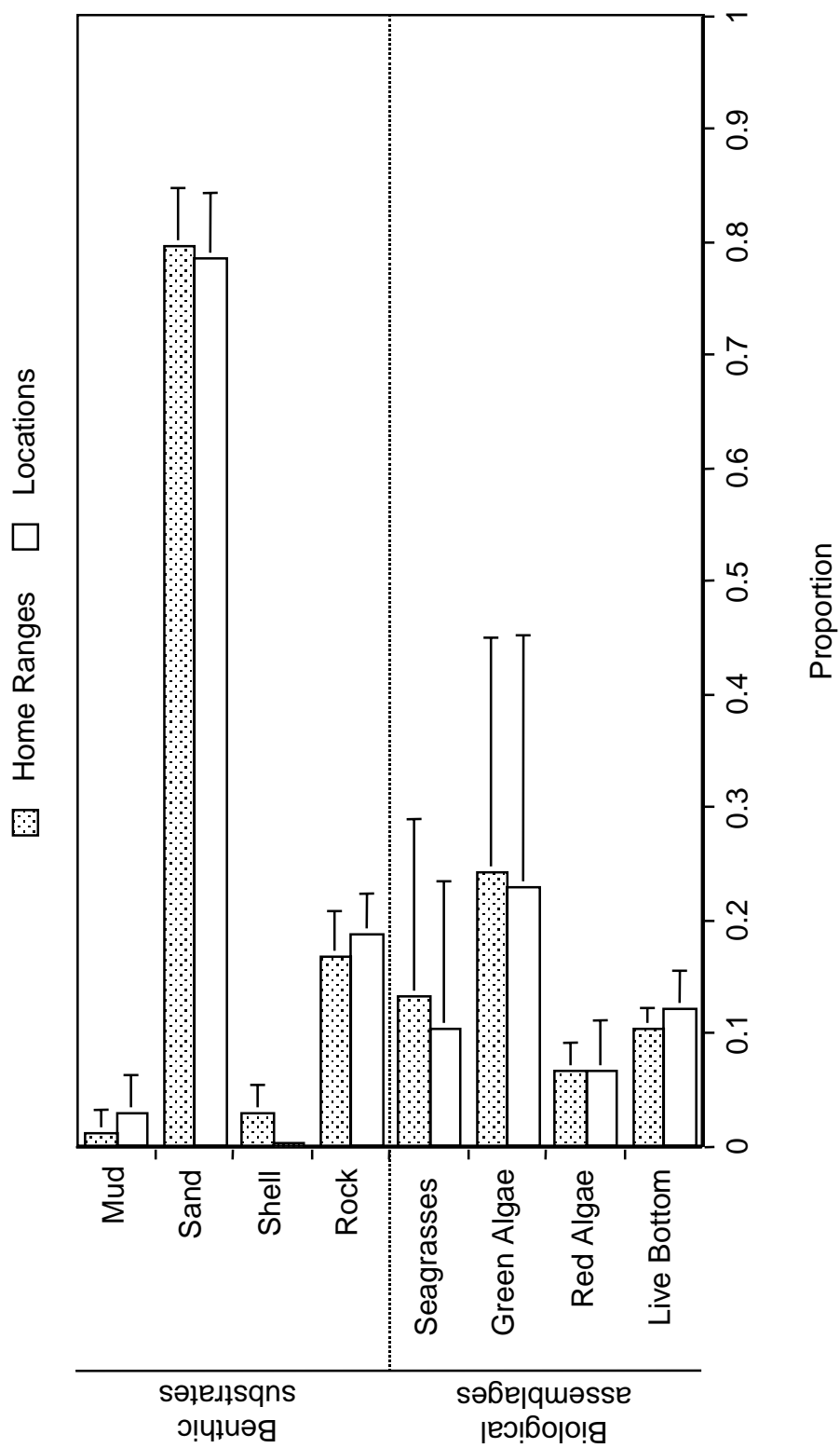


Figure 3-4. Mean compositions of benthic substrates and biological assemblages utilized by Kemp's ridley turtles.

Table 3-3. Compositional analyses of Kemp's ridley turtle habitat preference for combinations of benthic substrates (a – c) and individual biological assemblages (d – g). See [Appendix A](#) for the habitat compositions of each dataset.

Dataset	Order	χ^2	df	p-value	Rankings (significant differences in parentheses)
a) Primary substrates	Second	11.98	3	0.022	Rock>Sand>Shell>Mud (Rock & Sand >> Mud)
	Third	13.78	3	0.021	Rock>Mud>Sand>Shell (Rock & Sand >> Shell)
b) Substrates with rock	Second	17.29	6	0.154	Not significant
	Third	13.55	6	0.349	Not significant
c) Sand with rock	Second	14.11	4	0.043	Rock>SandRock>Sand>Shell>Mud (Rock, SandRock, & Sand >> Mud)
	Third	12.09	4	0.136	Not significant
d) Seagrass	Second	24.20	4	0.001	Rock>Sand>Shell>Seagrass>Mud (Rock & Sand >> Mud)
	Third	12.32	4	0.053	Not significant
e) Green algae	Second	28.42	4	0.001	Rock>Sand>Green>Shell>Mud (Rock & Sand >> Mud)
	Third	14.81	4	0.048	Mud>Rock>Sand>Green>Shell (Rock, Sand, & Green >> Shell)
f) Red algae	Second	21.79	4	0.004	Rock>Sand>Red>Shell>Mud (Rock & Sand>>Mud)
	Third	14.56	4	0.047	Mud>Rock>Sand>Red>Shell (Rock, Sand, & Red>>Shell)
g) Live bottom	Second	13.00	4	0.072	Not significant
	Third	13.58	4	0.051	Not significant

highest in significant third order analyses. Rock and sand were used significantly more than mud for all second order analyses and significantly more than shell for third order analyses. Furthermore, green and red macroalgae were used more than shell for third order analyses of individual biological assemblages.

For pairs of assemblages ([Table 3-4](#)), rock and live bottom were ranked highest in second order analyses, and mud was ranked highest in significant third order analyses. Rock, sand, live bottom, and red macroalgae were used significantly more than mud in second order analyses. Furthermore, live bottom, green macroalgae, and red macroalgae were used significantly more than seagrass. For significant third order analyses, shell was used significantly less than the other bottom types, and mud was utilized significantly more than seagrass in the green macroalgae-seagrass combination.

For combinations of three of the four biological assemblages ([Table 3-5](#)), rock and live bottom ranked highest in second order analyses, and mud ranked highest for the significant third order analysis of the green macroalgae-live bottom-red macroalgae combination. Live bottom was ranked the highest in the second order analysis of all biological assemblages combined. Rock, sand, live bottom, and red macroalgae were used significantly more than mud in second order analyses and significantly more than shell in the third order combination of seagrass-live bottom-red macroalgae. Furthermore, live bottom and green macroalgae were used significantly more than seagrass, and live bottom was used significantly more than red macroalgae, in second order analyses.

Table 3-4. Compositional analyses of Kemp's ridley turtle habitat preference for benthic substrates and paired biological assemblages. See [Appendix B](#) for the habitat compositions of each dataset.

Dataset	Order	χ^2	df	p-value	Rankings (significant differences in parentheses)
a) Seagrass-green algae	Second	29.45	5	0.005	Rock>Sand>Green>Shell>Seagrass>Mud (Rock & Sand>>Mud; Green>>Seagrass)
	Third	17.57	5	0.050	Mud>Sand>Rock>Green>Seagrass>Shell (Mud, Sand, Rock, & Green>>Shell; Mud>>Seagrass)
b) Seagrass-red algae	Second	24.61	5	0.014	Rock>Sand>Red>Shell>Seagrass>Mud (Rock, Sand, & Red>>Mud; Rock>>Red; Red>>Seagrass)
	Third	14.94	5	0.105	Not significant
c) Seagrass-live bottom	Second	25.89	5	0.004	Live>Rock>Sand>Shell>Seagrass>Mud (Live, Rock, & Sand>>Mud; Live>>Seagrass)
	Third	12.70	5	0.192	Not significant
d) Green algae-red algae	Second	34.51	5	0.002	Rock>Sand>Red>Green>Shell>Mud (Rock, Sand, & Red>>Mud)
	Third	16.48	5	0.085	Not significant
e) Green algae-live bottom	Second	31.87	5	0.003	Live>Rock>Sand>Green>Shell>Mud (Live, Rock, & Sand>>Mud)
	Third	15.06	5	0.123	Not significant
f) Red algae-live bottom	Second	21.53	5	0.012	Rock>Live>Sand>Red>Shell>Mud (Rock, Live, Sand, & Red>>Mud; Live>>Sand & Red)
	Third	18.92	5	0.026	Mud>Live>Sand>Rock>Red>Shell (Live, Sand, Rock, & Red>>Shell)

Table 3-5. Compositional analyses of Kemp's ridley turtle habitat preference for benthic substrates and tertiary combinations of biological assemblages (a - d) and all assemblages combined (e). See [Appendix C](#) for the habitat compositions of each dataset.

Dataset	Order	χ^2	df	p-value	Rankings (significant differences in parentheses)
a) Seagrass-green algae-red algae	Second	30.94	6	0.025	Rock>Sand>Red>Green>Shell>Seagrass>Mud (Rock, Sand, & Red>>Mud; Green>>Seagrass)
	Third	17.52	6	0.142	Not significant
b) Seagrass-green algae-live bottom	Second	31.70	6	0.017	Live>Rock>Sand>Green>Shell>Seagrass>Mud (Live, Rock, & Sand>>Mud; Live & Green>>Seagrass)
	Third	19.23	6	0.119	Not significant
c) Seagrass-red algae-live bottom	Second	30.63	6	0.023	Rock>Live>Sand>Red>Shell>Seagrass>Mud (Rock, Live, & Sand>>Mud; Live>>Seagrass & Red)
	Third	22.09	6	0.035	Mud>Live>Sand>Rock>Red>Seagrass>Shell (Live, Sand, Rock, & Red>>Shell)
d) Green algae-red algae-live bottom	Second	42.11	6	0.006	Live>Rock>Sand>Red>Green>Shell>Mud (Live, Rock, Sand, & Red>>Mud; Live>>Red)
	Third	14.72	6	0.285	Not significant
e) All biological assemblages	Second	36.39	7	0.049	Live>Rock>Sand>Red>Green>Shell>Seagrass>Mud (Live, Rock, Sand, & Red>>Mud; Live & Green>>Seagrass; Live>>Red)
	Third	26.24	7	0.136	Not significant

Depth Preference

Water depth in the study area ranged from exposed portions of Corrigan Reef in the north-central region to depths greater than 3.5 m in the extreme northwestern and southern regions (Fig. 3-5). Average depth was 1.8 ± 0.6 m, and there was a general trend for increasing depth from north to south. Most of the benthic substrates and components of the biological assemblages were collected in depths ranging from 1.0 to 2.5 m, except the oyster bars of Corrigan Reef and two species of green macroalgae, *C. sertularoides* and *A. crenulata*, collected in shallower waters (Table 3-6).

With the exception of LK4 and LK6, Kemp's ridley turtles typically utilized depths in the 1.0 - 2.0 m range (Fig. 3-6). The mean depths (Kruskal-Wallis, $p=0.0001$, and significant multiple comparisons) and depth distributions (Kolmogorov-Smirnov two sample tests, $p=0.0001$) at the locations of LK4 and LK6 were significantly greater than those of the other turtles. The locational depth distributions of the largest (LK2) and smallest (LK8) turtles were not significantly different (Kolmogorov-Smirnov, $p=0.78$). Furthermore, there was no significant correlation between carapace length and mean depth utilized by individual turtles (Spearman corr. coeff. = -0.213, $p=0.58$).

Second order analysis of 0.5 m depth intervals indicated a significant preference ($\chi^2=46.97$, $df=7$, $p=0.014$) for depth by Kemp's ridley turtles. Depth intervals were ranked as follows: 1.5-2.0 m > 1.0-1.5 m > 2.0-2.5 m > 0.5-1.0 m > Exposed > 2.5-3.0 m > 0.0-0.5 > 3.0+ m. Depths of 1.0 to 3.0 m were used significantly more than shallower or deeper depths (1.5-3.0 m >> 3.0+ m, 1.5-2.0

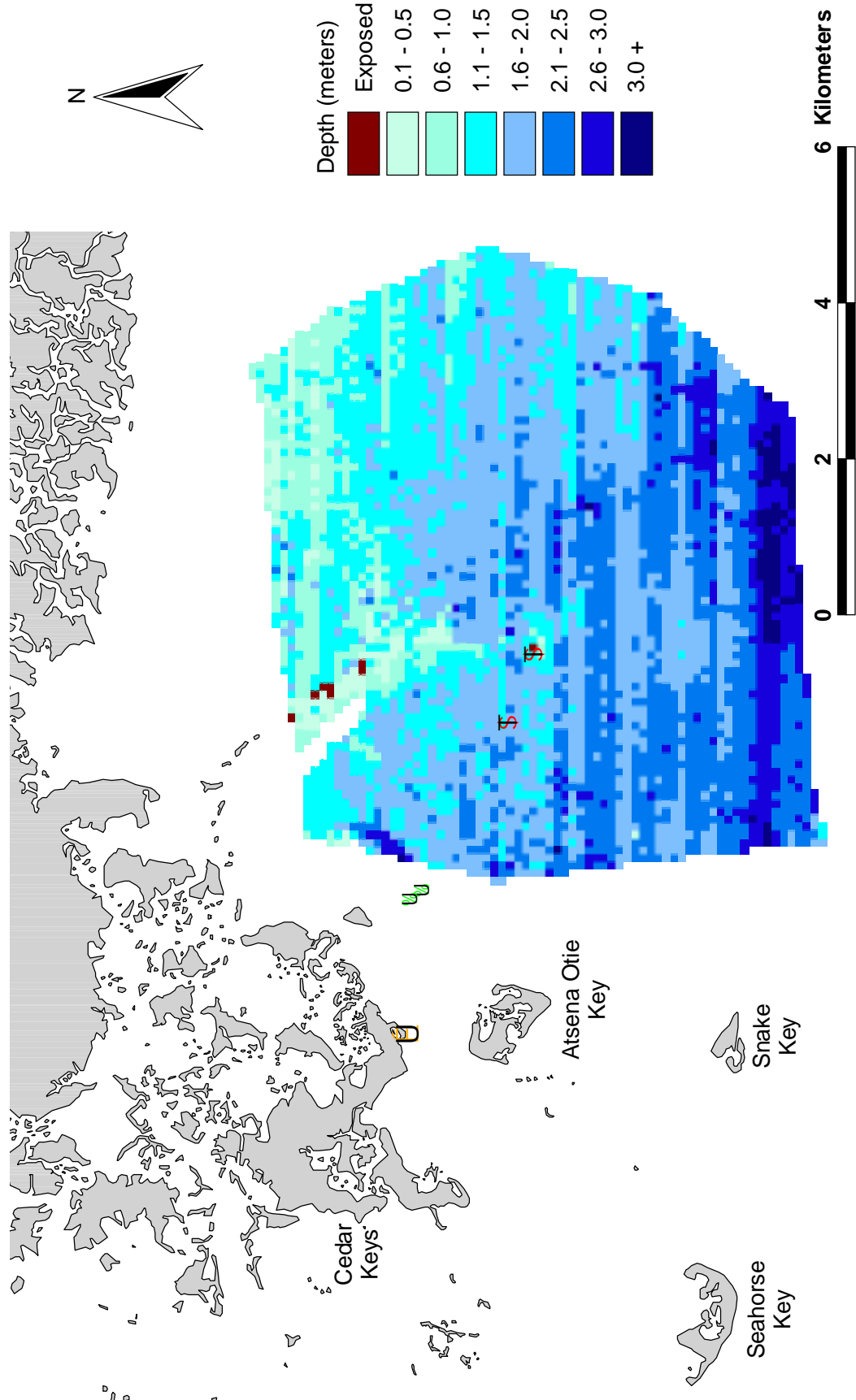


Figure 3-5. Bathymetric map of the study area. Squares and triangles represent channel markers and star denotes the location of the tide station.

Table 3-6. Percent depth distribution of benthic substrates and biological assemblages at 0.5 m intervals.

Bottom types	Depth intervals (m)									
	Exposed	0.1 - 0.5	0.6 - 1.0	1.1 - 1.5	1.6 - 2.0	2.1 - 2.5	2.6 - 3.0	> 3.0		
Benthic substrates										
Mud	0.0	0.0	11.7	58.5	21.3	7.4	1.1	0.0		
Sand	0.0	1.6	7.7	18.8	34.9	27.4	7.7	2.0		
Shell	6.8	35.9	29.1	24.3	2.9	1.0	0.0	0.0		
Rock	0.0	1.6	12.6	33.0	40.2	8.3	3.4	0.9		
Seagrasses										
<i>Halodule wrightii</i>	0.0	0.8	1.2	9.1	33.2	37.0	15.2	3.5		
<i>Halophila englemanni</i>	0.0	0.9	1.8	7.9	39.0	40.8	8.5	1.2		
<i>Syringodium filiforme</i>	0.0	0.0	1.7	10.2	44.1	35.6	8.5	0.0		
<i>Thalassia testudinum</i>	0.0	0.0	0.0	0.0	60.0	40.0	0.0	0.0		
Green Algae										
<i>Caulerpa prolifera</i>	0.0	1.0	7.4	16.4	35.2	29.2	8.4	2.4		
<i>C. mexicana</i>	0.0	0.5	0.0	1.8	35.2	45.7	13.2	3.7		
<i>C. sertularoides</i>	0.0	33.3	33.3	33.3	0.0	0.0	0.0	0.0		
<i>C. ashmeadii</i>	0.0	1.1	0.0	1.1	30.9	52.1	12.8	2.1		
<i>C. cupressoides</i>	0.0	0.0	0.0	4.8	19.0	40.5	31.0	4.8		
<i>Udotea conculata</i>	0.0	0.3	1.7	7.3	36.6	39.4	14.0	0.8		
<i>Acetabularia crenulata</i>	0.0	0.0	36.4	59.1	4.5	0.0	0.0	0.0		
<i>Halimeda incrassata</i>	0.0	0.0	0.0	6.9	36.2	44.8	10.3	1.7		
Red Algae										
<i>Gracilaria</i> spp.	0.0	1.2	10.6	26.0	33.3	24.8	3.8	0.3		
Brown Algae										
<i>Padina</i> sp.	0.0	0.0	7.1	35.7	28.6	14.3	7.1	7.1		
Live Bottom										
Sponges	0.0	1.7	10.0	26.8	34.0	19.6	5.8	2.1		
Gorgonians	0.0	0.0	7.8	36.3	37.3	13.7	4.9	0.0		
Bryozoans	0.0	0.0	8.3	8.3	58.3	19.4	2.8	2.8		
Tunicates	3.7	0.0	14.8	37.0	40.7	3.7	0.0	0.0		

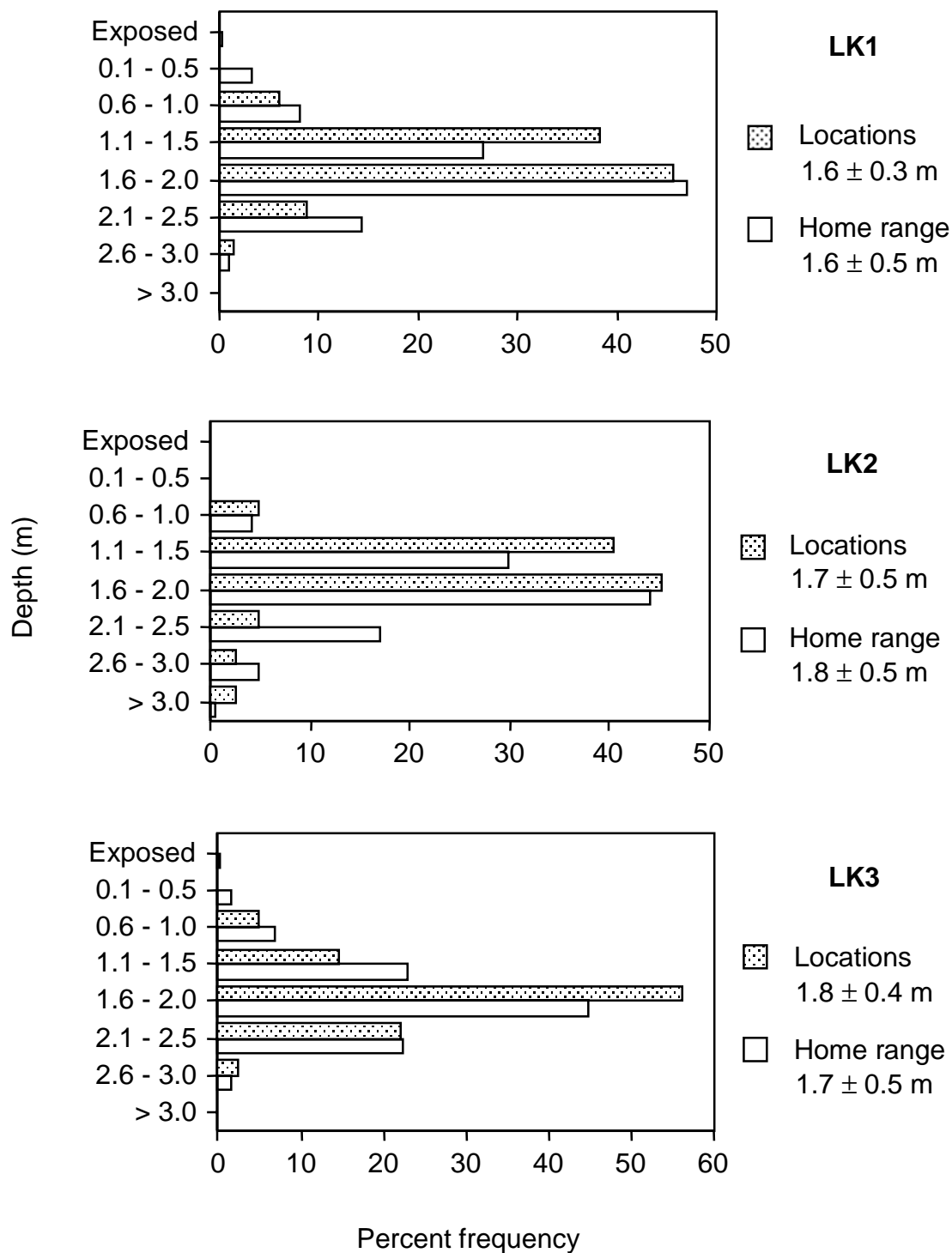


Figure 3-6. Frequency distribution of depth at the locations and in the home ranges of Kemp's ridley turtles. Means and standard deviations accompany the legends.

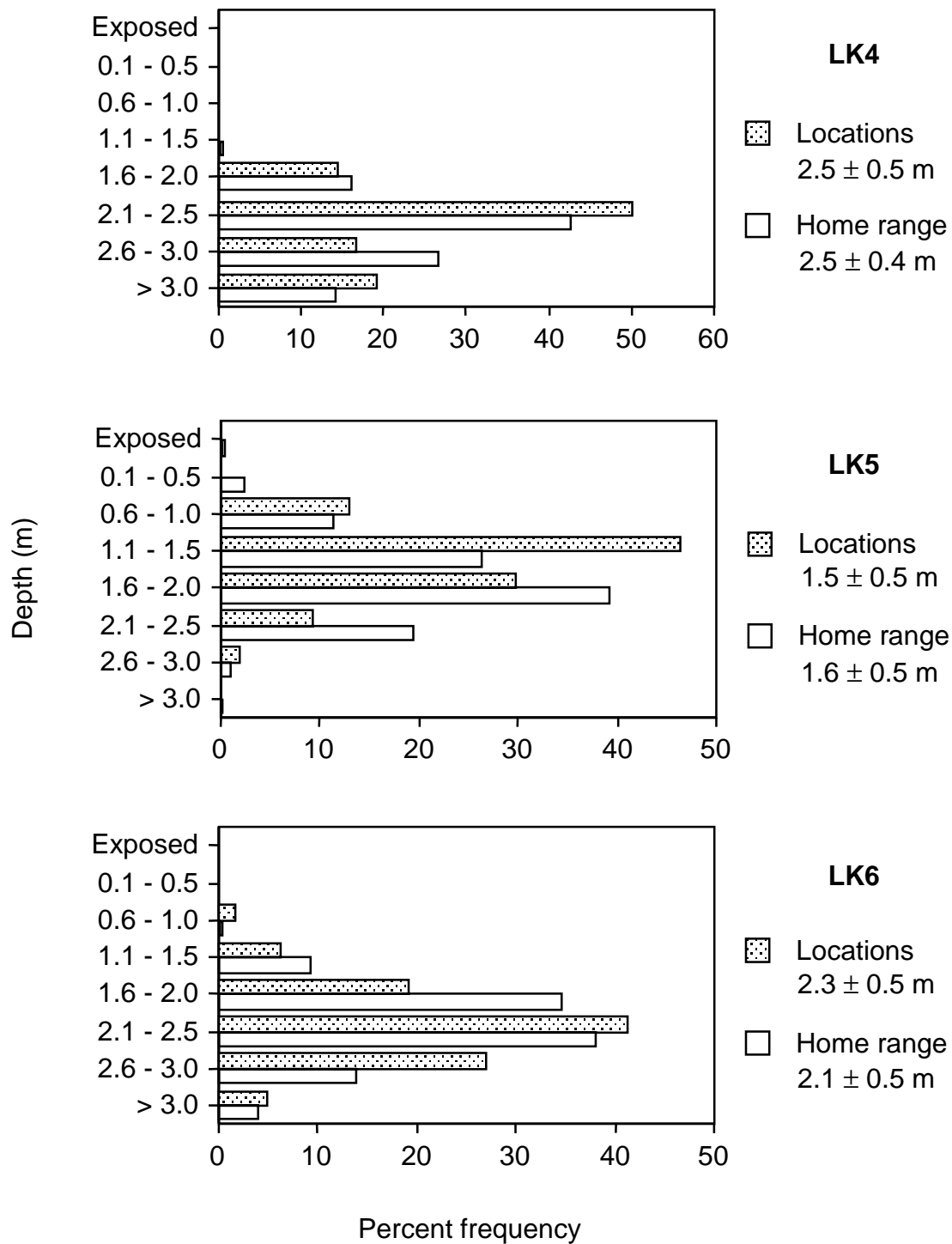


Figure 3-6. continued.

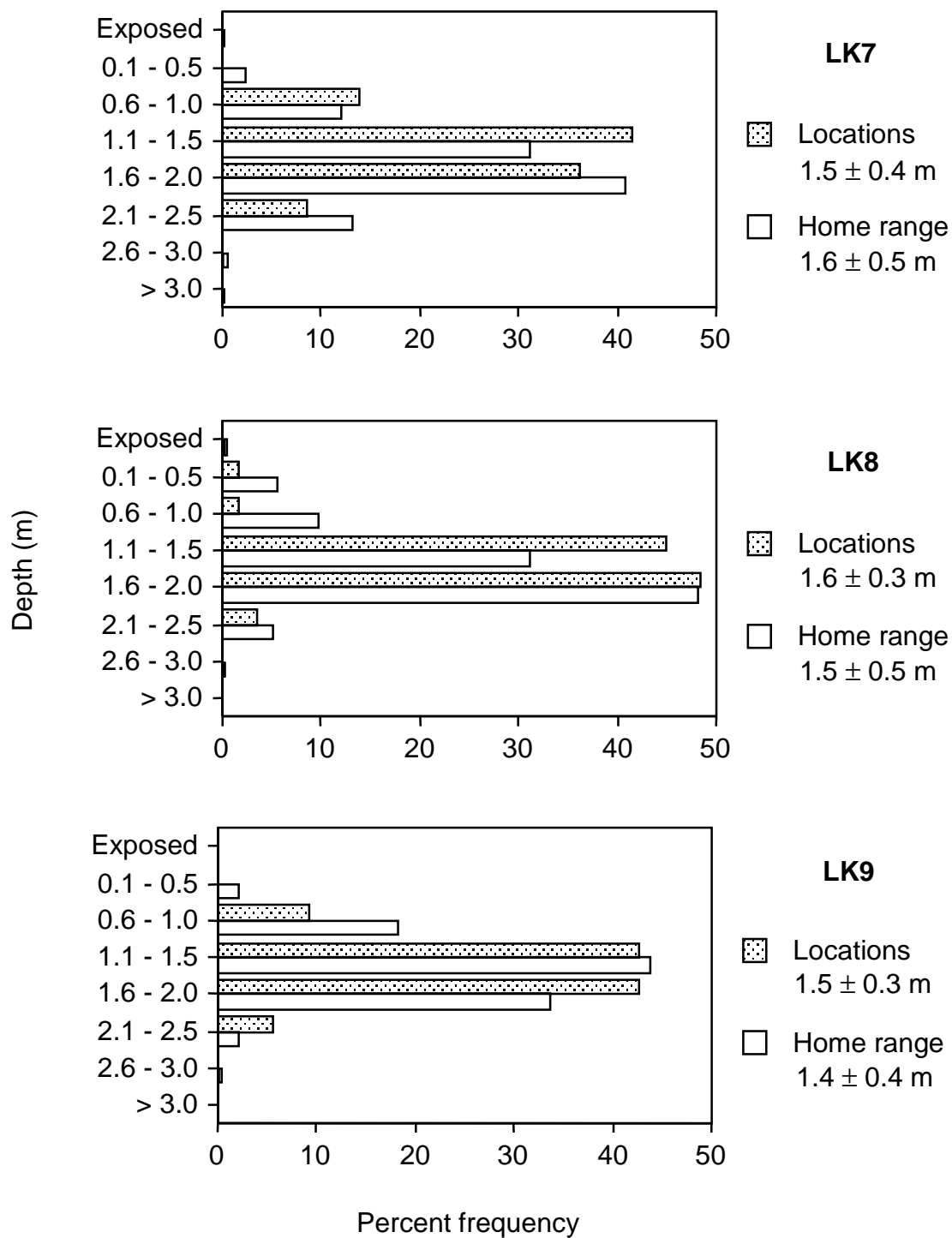


Figure 3-6. continued.

m >> Exposed, 2.0-2.5 m >> 2.5-3.0 m, and 1.0-1.5m>>0.5-1.0 m). Third order analysis of 0.5 m depth intervals was not significant ($\chi^2=22.73$, df=7, p=0.25).

Discussion

Kemp's ridley turtles are benthic carnivores, and, as such, would be expected to utilize the habitats of their prey (Ogren, 1989). Blue crabs (Portunidae; *Callinectes sapidus*) and stone crabs (Xanthidae; *Menippe* spp.) were prominent food items of the subadult turtles captured near the Cedar Keys (Schmid, 1998). Both crabs have been collected from a variety of the benthic substrates and biological assemblages (Powell and Gunter, 1968; Steele and Bert, 1994), but utilization of particular bottom types has been noted for each species. Juvenile and molting adult blue crabs conceal themselves in soft bottom seagrass (Orth and van Montfrans, 1990; Thomas et al., 1990; Wilson et al., 1990), and adult stone crabs are known to burrow in seagrass beds within the Cedar Keys archipelago (Bender, 1971). Juvenile stone crabs seek shelter within rocks and oyster shells, while the adults may also construct burrows in the soft substrate adjacent to these hard bottom structures (Powell and Gunter, 1968; McRae, 1950). Both crab species feed upon oysters (Eggleston, 1990; Brown and Haight, 1992), among many other things, and both commonly occur on the oyster reefs of northwestern Florida (Menzel and Nichy, 1958). However, Kemp's ridley turtles in the present study did not exhibit a high degree of utilization of seagrass or oyster habitat, as has been inferred in other telemetric and tagging

studies. Furthermore, compositional analyses indicated a preference for rock bottom, and the flora and fauna associated with this bottom type, which has not been suggested in any of the previous examinations of habitat associations. These unexpected results exemplify our lack of knowledge concerning the benthic ecology of Kemp's ridley turtles, and indicate the need for further research concerning the habitat preferences of this species.

Habitat architecture may have profound influences on the habitat selection and foraging behavior of a species ([Hacker and Steneck, 1990](#); [Parrish, 1995](#)). Therefore, the preference for hard bottom by Kemp's ridley turtles in the Cedar Keys may be a function of structural and spatial attributes of the available bottom types. The high relief and irregular surface of the Corrigan Reef oyster bars offer crabs greater protection from predation, as do the extensive seagrass beds on the eastern and western boundaries of the study area. By comparison, the limestone outcroppings are relatively flat with <1 m relief, and the associated macroalgal and epifaunal assemblages appear to be patchily distributed on and around the rock (Schmid, pers. obs.). Kemp's ridley turtles in this area may be selecting for less structurally complex habitats to optimize their detection and capture of prey. However, qualitative observations of foraging turtles are unattainable owing to the poor visibility in these turbid waters. Though logistically difficult, wild-caught turtles could be held in large aquariums, apparent differences among habitats could be replicated, and turtles could be subjected to experimental feeding trials to investigate the role of habitat architecture in their habitat preferences and foraging behavior.

Alternatively, the habitat associations of Kemp's ridley turtles in the Cedar Keys may reflect a greater abundance of prey in the rock habitat. Many species of decapod crustaceans utilize sessile invertebrate colonies, such as corals, tunicates, sponges, and bryozoans ([Collard and D'Asaro, 1973](#); [Lindberg, 1980](#); [Lindberg and Stanton, 1988](#)). [McRae \(1950\)](#) noted that the northwestern portion of the present study area contained limestone outcroppings with "corals" and sponges, and that young stone crabs were more abundant at this station than any other type of habitat sampled in the Cedar Keys. Interestingly, four of the Kemp's ridley turtles in the present study aggregated in this area. Most of the Kemp's ridley fecal samples collected in the Cedar Keys contained chelipeds of either stone crabs or blue crabs, not both. Individual turtles may feed selectively on a single crab species, which may account for the variation in habitat utilization within the study area. Turtles utilizing hard bottom assemblages may have been foraging on stone crabs, while turtles utilizing soft bottom assemblages may have been foraging on blue crabs. However, the inferred habitat preferences of the prey species have not been established, as was the case with the turtles prior to the present study. The possibility of habitat-specific prey selection could be investigated by establishing the habitat utilization of turtles via telemetric monitoring and then recapturing these individuals to analyze the contents of their feces. Areas utilized by telemetered turtles could be sampled to estimate the availability of prey items, and compositional analyses could be applied to determine if the turtles are exhibiting both habitat and food preferences.

Furthermore, habitat use-availability data could be collected for the two crab species to examine their habitat preferences in the study area.

The habitat utilization and preference of Kemp's ridley turtles observed in the present study could be an artifact of the initial capture location and the limited range of the study area. All the turtles were captured by Corrigan Reef and intensive monitoring was discontinued if a turtle traveled beyond a predetermined boundary (see [Materials and Methods section of Chapter 2](#)). Four turtles left the Cedar Keys study area and were therefore not included in the present analyses. One of the turtles moved eastward, possibly to the seagrass beds of Waccasassa Reefs, and two others moved westward, in a channel bisecting seagrass shoals within the Cedar Keys archipelago. However, all three of these turtles returned to the study area within a week, suggesting fidelity to previously utilized hard bottom sites. This fidelity could be tested by relocating turtles captured at Corrigan Reef to peripheral seagrass habitat and monitoring their movements to determine if they return to the study area. Additionally, similar-sized turtles should be captured in nearby seagrass habitats and telemetrically monitored to determine if these turtles exhibit comparable utilization and preference for hard bottom. The fourth turtle to leave the study area moved southward to deeper waters after the passage of a fall cold front, and may have left the Cedar Keys area shortly thereafter. Temperatures in the nearshore waters of the northern Gulf of Mexico decline with the onset of winter, and marine turtles must move to favorable thermal regimes to avoid mortality. Kemp's ridley turtles remigrate to Corrigan Reef between seasons and may continue to do so

for at least four years ([Schmid, 1998](#)). It would be of interest to determine if turtles return to previously utilized sites within the study area. However, the probability of recapturing a telemetered turtle between seasons is low. Such an endeavor would require a larger sample size of telemetered turtles and intensive netting efforts in subsequent years.

Telemetric data indicate that subadult Kemp's ridley turtles along the U.S. Atlantic and Gulf coasts migrate offshore and southward during winter months ([Gitschlag, 1996](#); [Renaud and Williams, 1997](#); [Morreale and Standora, 1998](#)), while adult females migrate to offshore areas in the northern and southern Gulf ([Byles, 1989](#)). However, there are no data on the offshore habitats utilized by this species. The preference for nearshore hard bottom communities observed in the present study may have important implications for the utilization of offshore winter habitats by subadults and the adults. The locations of hard bottom areas on the continental shelf of the southern Atlantic have been identified by the Southeast Area Monitoring and Assessment Program ([SEAMAP, 1999](#)). Despite differences in scale and resolution, a cursory examination of the SEAMAP data for southeast Florida and the movements of a telemetered Kemp's ridley turtle ([Gitschlag, 1996](#); Fig. 3) indicated that the turtle was in the vicinity of hard bottom areas south of Cape Canaveral from December through March. Scattered, low-relief outcrops of chert and limestone also occur in the shelf waters off western Florida and support a variety of macrobenthic fauna and macroalgal flora ([Brooks, 1973](#); [Collard and D'Asaro, 1973](#); [Humm, 1973](#)). A Kemp's ridley turtle was identified in a photographic survey of benthic communities in the waters off

southwest Florida ([Rosman et al., 1987](#)), but the time of year and the exact location of the sighting were not provided. Epibenthic communities also occur on rock outcrops, low-relief shell and gravel ridges, and relict carbonate reefs along the Mississippi-Alabama Shelf ([Brooks, 1991](#)) and the Texas-Louisiana Shelf ([Rezak et al., 1985](#)), particularly off Louisiana ([Gallaway, 1991](#)). All of these offshore hard-bottom areas have a warm-temperate environment during the winter, and may therefore provide winter refuge for subadult Kemp's ridley turtles. Similarly, adults may be utilizing hard bottom habitats in the northern Gulf, and those on the Yucatan-Campeche Shelf in the southern Gulf, as foraging grounds between nesting seasons. Satellite telemetry could be used to identify the offshore areas utilized by subadults and adults, and benthic sampling could be conducted in these areas to map the available bottom types. However, this telemetric method does not provide the locational accuracy needed to discern fine-scale habitat utilization, although transmitters are being developed that incorporate the exactness of the GPS navigational system.

[Ogren \(1989\)](#) characterized the life history of the Kemp's ridley turtle according to ontogenetic shifts in habitat utilization ([Fig. 3-7](#)): an epipelagic juvenile stage (< 20 cm SCL), a nearshore coastal-benthic subadult stage (20 - 60 cm SCL), and an offshore coastal-benthic adult stage (> 60 cm SCL). Kemp's ridley turtles inhabiting the Cedar Keys area have been characterized as mid- to late subadults (\bar{x} =44.5 cm SCL, range=26.8-58.6 cm, n=253; [Schmid, 1998](#)), and the telemetered turtles of the present study are representative of this aggregation. Significantly smaller (Kolmogorov-Smirnov 2-sample test, p=0.0001)

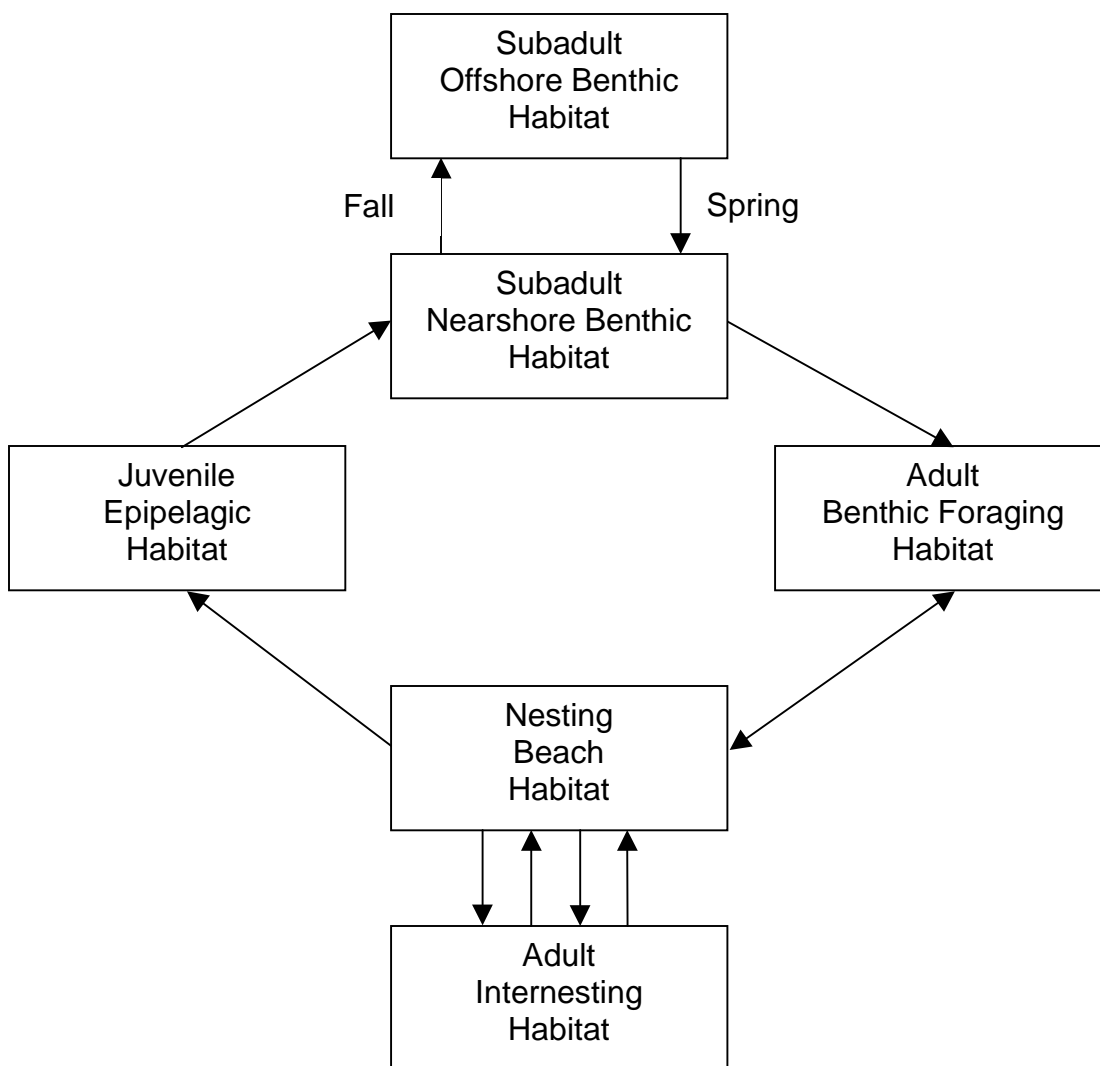


Figure 3-7. Life history model of Kemp's ridley turtle habitat utilization.

size classes of Kemp's ridley turtles are captured in Deadman Bay (\bar{x} = 32.7 cm SCL, range 20.7 - 51.8 cm, n = 63; Barichivich, unpubl. data; [Schmid and Barichivich, in prep.](#)), approximately 75 km northwest of the present study area. Capture data indicate that these early to mid-subadult turtles are utilizing seagrass habitat, and preliminary investigations on their feeding ecology indicate they are consuming spider crabs (Majidae; *Libinia* spp.; [Barichivich, 1998](#)). [Morreale and Standora \(1992, 1998\)](#) suggested that new recruits to the benthic environment feed selectively on slower-moving spider crabs rather than more abundant and faster-swimming lady crabs (Portunidae; *Ovalipes ocellatus*). Feeding on easily captured crab would reduce the time spent pursuing prey, and thus allow for the acquisition of more food per unit time assuming comparable abundance or densities. The amount of time turtles spent searching for prey would be decreased if spider crabs preferred the seagrass habitat. The distribution of *Libinia* has been correlated to a number of bottom types ([Williams, 1984](#)) and the food habits of *Libinia emarginata* have been described as herbivorous ([Ropes, 1988](#)), but there have been no studies of habitat preferences by spider crabs. On the contrary, the structural complexity of the seagrass habitat provides protection for decapod crustaceans ([Heck and Thoman, 1981](#)), which may increase prey search time by turtles and counter the benefits of reduced pursuit time. Therefore, the smaller Kemp's ridley turtles may select the shallow seagrass habitat owing to the protection from predators (e.g., sharks).

As Kemp's ridley turtles become more experienced and efficient in benthic foraging, their prey preferences may shift to the swimming crabs ([Morreale and Standora, 1992, 1998](#)). Eelgrass beds (*Zostera marina*) and blue crabs have been identified as the primary resources utilized by the Kemp's ridley turtles inhabiting Chesapeake Bay ([Lutcavage and Musick, 1985](#)), and the turtles in this region are larger ($\bar{x} = 41.0$ cm SCL; [Bytes, 1988](#)) than those captured in New England waters ($\bar{x} = 30.0$ cm SCL; [Standora et al., 1992](#)). Kemp's ridley turtles may become more adept at pursuing faster-moving portunid crabs in the seagrass habitat, but search time is still a factor. It has been demonstrated that densities of seagrass influence blue crab survival ([Wilson et al., 1987](#)). Higher predation rates were recorded for crabs in low- and high-density eelgrass beds while crabs in intermediate eelgrass densities experienced less predation. Correspondingly, Kemp's ridley turtles may select certain densities of vegetation when utilizing seagrass habitat in order to minimize time spent searching for prey. The role of seagrass architecture could be investigated telemetrically, as in the present study, or experimentally, as suggested earlier for the architecture among different bottom types.

Although a species may exhibit preference for a particular habitat, [Partridge \(1978\)](#) suggested that distribution among habitats is determined by inter- and intraspecific competition. Loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and Kemp's ridley turtles inhabit many of the same coastal areas. [Carr and Caldwell \(1956\)](#) reported concurrent captures of Kemp's ridley and green turtles on seagrass shoals off the Withlacoochee and Crystal Rivers,

approximately 35 km southeast of the Cedar Keys. The green turtle is herbivorous and, as such, forages in macroalgal and seagrass habitats. Kemp's ridley turtles may also utilize these vegetated habitats, but their carnivorous feeding strategy results in a partitioning of food sources between these species. Carr and Caldwell also indicated that loggerhead turtles were captured further offshore. [Byles \(1988\)](#) observed similar species-specific depth utilization in Chesapeake Bay. Kemp's ridley turtles occupied shallow (< 6 m) seagrass beds, while loggerhead turtles occupied deeper (> 6 m) waters in channels. [Lutcavage and Musick \(1985\)](#) also noted that Kemp's ridley turtles fed on blue crabs and loggerhead turtles fed on horseshoe crabs (*Limulus polyphemus*). Byles concluded that the differences in habitat, behavior, and prey items amounted to resource partitioning between the species. Kemp's ridley turtles had the highest relative abundance at Corrigan Reef, but loggerheads were occasionally captured in the same locations at the same time ([Schmid, 1998](#)). This indicates that the loggerhead turtle does have access to the preferred habitat of Kemp's ridley turtles in the Cedar Keys study area. If both species are competing for the same resources, the loggerhead turtle may be the dominant species by virtue of its greater size (50 - 80+ cm SCL; [Schmid, 1998](#)) and may therefore displace the Kemp's ridley turtle to less preferred habitat. However, the larger size of the loggerhead turtles may also necessitate utilization of deeper waters. A telemetric investigation of loggerhead turtles is needed to establish their habitat and depth preferences in the Cedar Keys area, and to investigate possible competition for habitat with Kemp's ridley turtles. Furthermore, fecal specimens should be

collected from both species captured at Corrigan Reef in order to compare prey items. [Dunham \(1980\)](#) indicated that comparing patterns of resource utilization is useful in formulating hypotheses, but the experimental manipulation of natural populations, through selective removal or addition of individuals, is a more powerful method for testing predictions of competition theory. In the case of Kemp's ridley and loggerhead turtles, however, the complete removal of either species would be problematic in a large and open embayment such as Waccasassa Bay.

Other than nesting aggregations, there is no information on interactions among wild Kemp's ridley turtles. A number of turtles would have to be observed or telemetered simultaneously in order to examine the possibility of intraspecific competition. Nonetheless, general statements can be made concerning their distribution among foraging habitats. Post-pelagic Kemp's ridley turtles appear to utilize seagrass habitat and may continue to do so through the mid-subadult stage. These smaller size classes may also recruit to nearshore hard bottom areas, but would face competition with larger conspecifics already established in this habitat type. Therefore, the utilization of seagrass habitat may reflect intraspecific competitive exclusion in addition to the protection from predation suggested earlier. Larger size classes of subadult Kemp's ridley turtles could also utilize the seagrass habitat, but develop a preference for nearshore hard bottom communities. This may be an innate preference for habitat or learned from the distribution of their prey. The shift in habitat utilization may also correspond to the onset of pubertal changes. [Gregory and Schmid \(in review\)](#) indicated that Kemp's

ridley turtles may begin maturing at approximately 40 cm SCL, and, as suggested by [Coyne and Landry \(in press\)](#), reclassified [Ogren's \(1989\)](#) coastal-benthic immature stage as a 20 - 40 cm pre-pubertal stage and a 40 - 60 cm pubertal stage. Correspondingly, pre-pubertal turtles in the northeastern Gulf may prefer seagrass communities, while the maturing turtles in the Cedar Keys prefer epibenthic communities associated with hard bottom. [Carr and Caldwell \(1958\)](#) indicated that larger, adult-size Kemp's ridley turtles were once captured further offshore along the west coast of Florida. Therefore, mature turtles appear to shift their habitat utilization to offshore areas, possibly hard bottom, but could still have access to nearshore sites. These observations suggest that distribution among habitats by larger size classes of Kemp's ridley turtles may be the result of ontogenetic changes rather than intraspecific competition.

As suggested earlier for loggerheads, the larger body size of mature Kemp's ridley turtles may necessitate the utilization of deeper depths, and observational data support size-specific depth utilization. [Ogren \(1989\)](#) suggested that the physiological diving constraints of smaller Kemp's ridley turtles might limit them to shallow-water habitats. Kemp's ridley turtles in the present study utilized depths less than 4 m and demonstrated a preference for areas of 1-2 m depth. There was no apparent trend in depth utilization across the size range of telemetered turtles, but post-pelagic (20-25 cm SCL) and early subadult (25-35 cm SCL) turtles were not represented in this sample. These smaller turtles may be utilizing shallower depths than those documented for the larger turtles in the present study. Future telemetric studies should include early

subadult and adult size classes to investigate the possibility of size-specific habitat and depth preferences by Kemp's ridley turtles.

Management Implications

The number of nesting Kemp's ridley turtles has steadily increased in recent years, presumably owing to the protection of the primary nesting beach and restrictions designed to decrease mortality in commercial fisheries ([Márquez et al., 1996](#); [Turtle Expert Working Group, 1998](#)). Nonetheless, the status of the Kemp's ridley turtle remains precarious as nesting intensity is still well below historical levels. Increases in the number of hatchlings released from the hatchery program have presumably led to increased numbers of subadult turtles in U.S. coastal waters ([Ogren, 1989](#); [Ross et al., 1990](#); [Schmid, 1998](#)). As subadult abundance continues to increase, the availability of preferred habitat and prey will become increasingly important in maintaining a viable population of Kemp's ridley turtles. The present study is the first to conduct a detailed analysis of the habitat preferences of Kemp's ridley turtles and the benthic habitats in which they forage. Similar studies are needed throughout their distribution to investigate regional and developmental differences in habitat availability, utilization, and preference of both habitat and prey. Recovery plans can then incorporate the results of these studies to protect or enhance the preferred resources of Kemp's ridley turtles.

A major concern in the recovery of this endangered species is habitat degradation resulting from coastal development, industrial pollution, channel

construction and maintenance, and petroleum exploration and extraction ([U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992](#)). A number of coastal areas in the U.S. are already protected as federal and state lands. The study area for the present investigation is bounded by the Cedar Keys National Wildlife Refuge and the Waccasassa Bay State Preserve. However, past efforts to establish a marine sanctuary in the sparsely developed Big Bend area of Florida were unsuccessful. Although it may not have been feasible to designate entire stretch of coastal waters as sanctuaries for subadult Kemp's ridley turtles, perhaps smaller reserves could be established in areas of aggregation.

There are important considerations when designing a marine reserve system for species with stage-structured life histories ([St. Mary et al., in press](#)). For example, Kemp's ridley turtles may occupy three distinct and spatially separate habitats during the subadult stage: nearshore seagrass beds, nearshore hard bottom, and offshore winter habitat, possibly hard bottom. Conservation of marine habitat in Florida has focused on the protection of nearshore coral reefs and seagrass beds, the latter of which would benefit smaller size classes of subadult Kemp's ridley turtles. However, stage-based population models indicate that the larger size classes of immature turtles are more sensitive to mortality and, as such, should be considered in management plans ([Crouse et al., 1987](#)). Therefore, attention should also be given to the nearshore hard bottom areas that are preferred by larger size classes of Kemp's ridley turtles. Long-term and concurrent tagging studies are also needed to

demonstrate the ontogenetic shift in habitat utilization and the subsequent coupling among habitat types.

CHAPTER 4 SUMMARY

Subadult Kemp's ridley turtles are distributed in the coastal waters of the U.S. from Massachusetts to Texas. Tagging studies have characterized regional aggregations of subadults and provided information on their migrations and local movements. Telemetric studies have been employed to fill data gaps between the release of tagged turtles and their subsequent recapture. Despite long-term tagging studies in western Florida, there is very little information on the behavior and local movements of Kemp's ridley turtles in this region. The purpose of the present study was to investigate the activity patterns and habitat associations of Kemp's ridley turtles in the Cedar Keys area of west-central Florida.

Activity Patterns

Radio and sonic telemetry were used to determine the extent to which Kemp's ridley turtles exhibit site fidelity, to determine if their movements were correlated with tidal flow, to describe their rate of movement and respiratory behavior and determine if these patterns changed with respect to time of day, and to determine if these latter activities were correlated with one another and body mass. Five turtles were instrumented in 1994 and 10 in 1995, but only

turtles with > 40 hours radio monitoring (n=7) or > 40 locations (n=9) were used in the analyses.

Kemp's ridley turtles exhibited strong fidelity to areas peripheral to the Corrigan Reef oyster bar complex. Approximately half of the turtles occupied small foraging ranges (5 - 13 km²), while the remaining turtles occupied larger areas (18 - 30 km²) resulting from periodic increases of 10 - 20 km². Home range area was not significantly correlated with body size. Two turtles with the smallest foraging ranges were multiannual recaptures from tagging studies conducted 3 - 4 years earlier. Telemetered turtles remained within the study area for weeks to months, and 3 of the 4 turtles that left the study area returned within a week.

Kemp's ridley turtles typically traveled with the direction of tidal flow. The mean of mean turtle bearings on incoming ($48 \pm 49^\circ$) and falling ($232 \pm 41^\circ$) tides were significantly oriented to the mean direction of tidal flow recorded in 1995 (37° , $p < 0.0025$, and 234° , $p < 0.005$, respectively). Turtles also traveled perpendicular to tidal flow and exhibited extended periods of little or no directed movement, both of which resulted in decreased mean vector lengths and increased angular deviations.

Mean rate of movement (ROM) for all turtles combined was 0.437 ± 0.331 km/hr (range: 0.004 - 1.758 km/hr), and means for individual turtles ranged from 0.274 to 0.600 km/hr. ROM differed significantly among turtles, but there were no indications of increasing ROM with increasing body size. Only turtles tracked in 1995 (n=5) had sufficient 24 hr data to test for time interval patterns of ROM. There was a trend for higher mean ROM during the day, but the difference was

only significant for one turtle. Mean ROM was significantly greater on the falling tide for all turtles combined, despite the trend for higher tidal velocities on the incoming tide. ROM and tidal velocity were significantly correlated for both tidal states.

A mean surface duration of 18 ± 15 seconds (range: 1 - 88 seconds) and a mean submergence duration of 8.4 ± 6.4 minutes (range: 0.2 - 60.0 minutes) were calculated for all turtles combined. Surface durations and submergence durations were significantly different ($p=0.0001$) among turtles. Mean surface durations were shorter during the night for turtles tracked in 1994 and shorter during the day for turtles tracked in 1995. Mean submergence durations were significantly longer during the 12-hour and 8-hour nights for all turtles combined.

Respiratory activities of all Kemp's ridley turtles combined were significantly correlated with ROM. Mean hourly surface and submergence durations decreased with increasing ROM and the number of surfacings per hour increased with increasing ROM, although the significance of these relationships varied among turtles.

One of the telemetered turtles not included in the analyses moved southward to relatively deeper waters after the passage of a cold front in November. It is not known whether Kemp's ridley turtles continue to move southward along the coast as temperatures decrease in nearshore waters or if they move to the deeper, warmer waters offshore. Satellite telemetry should be used to investigate the seasonal activity patterns of Kemp's ridley turtles in the northeastern Gulf of Mexico.

Habitat Analyses

Habitat associations of Kemp's ridley turtles were analyzed in terms of availability of benthic habitats, utilization of habitat by turtles, and preference for a particular habitat type. Benthic samples were collected to characterize the bottom types within the study area and a geographic information system was used to map the benthic habitats and determine their availability. Locational data of turtles collected via telemetry were overlaid on the habitat map in order to estimate habitat utilization. Compositional analyses were performed on the availability and utilization proportions in two stages to determine if turtles preferred a particular bottom type or depth within their foraging ranges or within the study area.

The intertidal oyster reefs and shell bars of Corrigan Reef are prominent geographic features in the northern region of the Cedar Keys study area, but accounted for a small percentage (< 2%) of the overall habitat composite. Unvegetated sand was the dominant bottom type, comprising 48% of the entire study area. However, over half of the sand sites had rock outcroppings. The southern and, to a lesser extent, the eastern regions of the study area were composed of subtidal seagrass and green macroalgae meadows, which together accounted for 28% of the total available habitat. The seagrass assemblage was a soft bottom community, while the green macroalgae assemblage was more of a hard bottom community. Live bottom and red macroalgae were distributed throughout the study area as hard bottom assemblages and each comprised 7% of the total habitat composite. The availability of hard bottom assemblages within

the study area was probably underestimated given the preponderance of rock outcroppings in sites classified as sand.

Kemp's ridley turtles utilized unvegetated sand the most (80% of home ranges and 79% of locations), but over 50% of the utilized sand sites had rock outcroppings. Green algae had the highest proportion of utilization for biological assemblages (24% and 23%), followed by seagrasses (13% and 10%) and live bottom (10% and 12%). Six of the turtles utilized unvegetated, rocky sand bottom (65 - 78% of foraging ranges and 64 - 82% of locations) peripheral to Corrigan Reef. The remaining 3 turtles utilized vegetated bottom (37 - 64% and 31 - 57%), primarily green macroalgae, in the deeper southern region of the study area.

Compositional analyses of habitat preference indicated that Kemp's ridley turtles used rock outcroppings in their foraging ranges at a significantly higher proportion than available within the study area. In addition, live bottom and green macroalgae assemblages in the foraging ranges of turtles were preferred over the seagrass assemblage. The locational data within the foraging ranges of five turtles also indicated a preference for mud bottom occurring on the periphery of Corrigan Reef in the extreme northern region of the study area.

Water depth ranged from intertidal portions of Corrigan Reef in the north-central region of the study area to depths > 3 m in the northwestern and southern regions, but turtles typically utilized and preferred 1-2 m depths within their foraging ranges. There was no significant correlation between mean depth utilized and the carapace length of the turtles, but smaller size classes were not represented in this sample.

The life history of the Kemp's ridley turtle includes ontogenetic shifts in habitat and prey, but very little is known about resource utilization by this species. Other studies have inferred utilization of seagrass and oyster habitats by subadult turtles, but the present investigation is the first to demonstrate a preference for hard bottom areas and the associated macroalgal flora and epifauna. Variability in the habitats utilized by turtles may be the result of individual prey preferences. This supposition could be investigated by: 1) tracking turtles to establish habitat utilization, 2) recapturing turtles and collecting fecal samples to determine prey utilization, 3) sampling areas utilized by turtles to determine prey availability, and 4) comparing the use-availability data to determine habitat-specific prey preferences. Additionally, smaller size classes of turtles may utilize habitats other than those documented in the present study and should be included in future investigations of the habitat associations of this species.

LITERATURE CITED

- Ackerman, B. B., F. A. Leban, M. D. Samuel, and E. O. Garton. 1990. User's Manual for Program HOME RANGE. 2nd ed. Technical Report 15, Forestry, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID. 80 p.
- Aebischer, N. J. and P. A. Robertson. 1992. Practical aspects of compositional analysis as applied to pheasant habitat utilization. *In*: I. G. Priede and S. M. Swift, Wildlife Telemetry: Remote Monitoring and Tracking of Animals, Ellis Horwood, New York. pp. 272-284.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Agee, J. K., S. C. F. Stitt, M. Nyquist, and R. Root. 1989. A geographic analysis of historical grizzly bear sightings in the North Cascades. *Photogramm. Engrg. Remote Sens.* 55:1637-1642.
- Aitchison, J. 1986. *The Statistical Analysis of Compositional Data*. Chapman and Hall, New York. 416 p.
- Allredge, J. R. and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 50:157-165.
- Ambrose, C. E. 1998. Manatee and habitat: a geographic information system (GIS) perspective. Ph.D. dissertation, Florida Institute of Technology, Melbourne, FL. 140 p.

- Andersen, D. E. and O. J. Rongstad. 1989. Home-range estimates of red-tailed hawks based on random and systematic relocations. *J. Wildl. Manage.* 53:802-807.
- ASTM, 1993. Standard test method for the amount of materials in soils finer than the no. 200 (75 μ m) sieve. *In: Annual Book of ASTM Standards, Section 4, Vol. 04.08, American Society for Testing and Materials, Philadelphia, PA.* pp. 191-193.
- Baldwin, H. A., D. L. Brumbaugh, and A. Carr. 1969. Initial experiments with migrating *Chelonia mydas* using telemetry. Preliminary Technical Report, Office of Naval Research. Contract NONR-4315(00). 33 p.
- Barichivich, W. J. 1998. Feeding ecology and habitat affinities of Kemp's ridley sea turtles (*Lepidochelys kemp*) in the Big Bend, Florida. Annual report to National Marine Fisheries Service, Panama City, FL. December, 1998. 18 p.
- Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, New York. 371 p.
- Bellmund, S. A., J. A. Musick, R. C. Klinger, R. A. Byles, J. A. Keinath, and D. E. Barnard. 1987. Ecology of sea turtles in Virginia. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. Special Scientific Report No. 119. 48p.
- Bender, E. S. 1971. Studies of the life history of the stone crab, *Menippe mercenaria* (Say), in the Cedar Key area. M.S. thesis, University of Florida, Gainesville, FL. 110 p.
- Bjorndal, K. A. 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar. Biol.* 56:147-154.
- Bjorndal, K. A. and A. B. Bolten. 1990. Goals for sea turtle research in the Gulf of Mexico with respect to the oil and gas industries. *In: Tucker and Associates, Inc., Sea Turtles and Marine Mammals of the Gulf of Mexico, Proceedings of a Workshop Held in New Orleans, August 1-3, 1989.* OCS Study MMS 90-0009:47-58.

- Bolten, A. B. and H. R. Martins. 1990. Kemp's ridley captured in Azores. *Mar. Turtle Newsl.* 48:23.
- Bolten, A. B. 1999. Techniques for measuring sea turtles. *In*: K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly (eds.), *Research and Management Techniques for the Conservation of Sea Turtles*. IUCN/SSC Marine Turtle Specialist Group Publication No. 4. pp. 110-114.
- Breining, D. R., M. J. Provancha, and R. B. Smith. 1991. Mapping Florida scrub jay habitat for purposes of land-use management. *Photogramm. Engrg. Remote Sens.* 57:1467-1474.
- Brongersma, L. D. 1982. Marine turtles of the eastern Atlantic Ocean. *In*: K. A. Bjorndal (ed.), *Biology and Conservation of Sea Turtles*. Smithsonian Institution Press, Washington, DC. pp. 407-416.
- Brooks, G. R. and L. J. Doyle. 1998. Recent sedimentary development of Tampa Bay, Florida: a microtidal estuary incised into tertiary platform carbonates. *Estuaries* 21:391-406.
- Brooks, H. K. 1973. The physical environment: geological oceanography. *In*: J. I. Jones, R. E. Ring, M. O. Rinkel, and R. E. Smith (eds.), *A Summary of the Knowledge of the Eastern Gulf of Mexico*. State University System of Florida, Institute of Oceanography, St. Petersburg, FL. pp. IIE-1 - IIE-49.
- Brooks, J. M. (ed.). 1991. Mississippi-Alabama Continental Shelf Ecosystem Study: Data Summary and Synthesis, Volume I: Executive Summary. U.S. Dept. of the Interior, Minerals and Management Service, Gulf of Mexico OCS Regional Office, New Orleans, LA. OCS Study MMS 91-0062. 43 p.
- Brown, K. M. and E. S. Haight. 1992. The foraging ecology of the Gulf of Mexico stone crab *Menippe adina* (Williams et Felder). *J. Exp. Biol. Ecol.* 160:67-80.
- Burchfield, P. M., R. Byles, J. V. Mongrell, M. Bartlett, and D. Rostal. 1988. Report on Republic of Mexico/United States of America conservation effort on behalf of Kemp's ridley sea turtle at Playa de Ranch Nuevo, Tamaulipas, Mexico, 1988. Gladys Porter Zoo, Brownsville, TX. 83 p.

- Butler, P. J., W. K. Milsom, and A. J. Woakes. 1984. Respiratory, cardiovascular and metabolic adjustments during steady state swimming in the green turtle, *Chelonia mydas*. J. Comp. Physiol. 154B:167-174.
- Byles, R. A. 1988. Behavior and ecology of sea turtles from Chesapeake Bay, Virginia. Ph.D. Dissertation, Virginia Institute of Marine Science, College of William and Mary, Williamsburg, VA. 112 p.
- Byles, R. A. 1989. Satellite telemetry of Kemp's ridley sea turtle, *Lepidochelys kempii*, in the Gulf of Mexico. In: S. A. Eckert, K. L. Eckert, and T. H. Richardson, (comps.), Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232:25-26.
- Byles, R. A. and P. T. Plotkin. 1994. Comparison of the migratory behavior of congeneric sea turtles *Lepidochelys olivacea* and *L. kempii*. In: B. A. Schroeder and B. E. Witherington, (comps.), Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-341:39.
- Carr, A. F., Jr. 1942. Notes on sea turtles. Proc. New England Zool. Club 21:1-16.
- Carr, A. 1963. Panspecific reproductive convergence in *Lepidochelys kempii*. Ergeb. Biol. 26:298-303.
- Carr, A. 1980. Some problems of sea turtle ecology. Am. Zool. 20:489-498.
- Carr, A. F. and D. K. Caldwell. 1956. The ecology and migrations of sea turtles: 1. Results of field work in Florida, 1955. Am. Mus. Nov. 1793:1-23.
- Carr, A. and D. K. Caldwell. 1958. The problem of the Atlantic ridley turtle (*Lepidochelys kempii*) in 1958. Rev. Biol. Trop. 6:245-262.
- Carroll, J. P., R. D. Crawford, and J. W. Schulz. 1995. Gray partridge winter home range and use of habitat in North Dakota. J. Wildl. Manage. 59:98-103.

- Carter, S. L., C. A. Haas, and J. C. Mitchell. 1999. Home range and habitat selection of bog turtles in southwestern Virginia. *J. Wildl. Manage.* 63:853-860.
- Chaloupka, M. and G. R. Zug. 1997. A polyphasic growth function for the endangered Kemp's ridley sea turtle, *Lepidochelys kempii*. *Fish. Bull.* 95:849-856.
- Cloudsley-Thompson, J. L. 1961. Rhythmic Activity in Animal Physiology and Behaviour. Academic Press, New York. 236 p.
- Collard, S. B. 1990. The influence of oceanographic features on post-hatchling sea turtle distribution and dispersion in the pelagic environment. *In*: T. H. Richardson, J. I. Richardson, and M. Donnelly (comps.), Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278:111-114.
- Collard, S. B. and C. N. D'Asaro. 1973 The biological environment: benthic invertebrates of the eastern Gulf of Mexico. *In*: J. I. Jones, R. E. Ring, M. O. Rinkel, and R. E. Smith (eds.), A Summary of the Knowledge of the Eastern Gulf of Mexico. State University System of Florida, Institute of Oceanography, St. Petersburg, FL. pp. IIIG-1 - IIIG-27.
- Collard, S. B. and L. H. Ogren. 1990. Dispersal scenarios for pelagic post-hatchling sea turtles. *Bull. Mar. Sci.* 47:233-243.
- Colton, D. E. and W. S. Alevizon. 1983. Movement patterns of bonefish, *Albula vulpes*, in Bahamian waters. *Fish. Bull.* 81:148-154.
- Continental Shelf Associates, Inc. and Martel Laboratories Inc. 1985. Florida Big Bend Seagrass Habitat Study Narrative Report. A final report by Continental Shelf Associates, Inc. submitted to the Minerals Management Service, Metairie, LA. Contract No. 14-12-001-30188.
- Coyne, M. S. and Landry, A. M. in press. Plasma testosterone sexing criteria and sex ratio of the Kemp's ridley sea turtle (*Lepidochelys kempii*). *In*: F.A. Abreu-Grobois, R. Briseño-Dueñas, R. Márquez, and L. Sarti (comps.),

Proceedings of the Eighteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memo.

- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412-1423.
- Daniel, W. W. 1990. Applied Nonparametric Statistics, 2nd ed. PWS-KENT, Boston, MA. 635 p.
- Danton, C. and R. Prescott. 1988. Kemp's ridley in Cape Cod Bay, Massachusetts-1987 field research. *In*: B. A. Schroeder (comp.), Proceedings of the Eighth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-214:17-18.
- Dodd, C. K., Jr. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). U.S. Fish Wildl. Serv., Biol. Rep. 88(14). 110 p.
- Dunham, A. E. 1980. An experimental study of interspecific competition between the iguanid lizards *Sclerophorus merriami* and *Urosaurus ornatus*. *Ecol. Monogr.* 50:309-330.
- Eckert, S. A., K. L. Eckert, P. Ponganis, and G. L. Kooyman. 1989. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.* 67:2834-2840.
- Eggleston, D. B. 1990. Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: effects of prey density and size. *Bull. Mar. Sci.* 46:62-82.
- Ehrhart, L. M. 1980. A continuation of base-line studies for environmentally monitoring space transportation systems (STS) at the John F. Kennedy space center. Vol. 4: threatened and endangered species of the Kennedy Space Center. Part 1: marine turtle studies. Final Report, 1976-1979. 417 p.

- Epperly, S. A., J. Braun, and J. A. Collazo. 1995. Application of sonic telemetry for identification of critical habitat of turtles. *In*: J. A. Keinath, D. E. Barnard, J. A. Musick and B. A. Bell (comps.), Proceedings of the Fifteenth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFSC-387:84-87.
- Fretwell, S. D. and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19:16-36.
- Gitschlag, G. M. 1996. Migration and diving behavior of Kemp's ridley (Garman) sea turtles along the U.S. southeastern Atlantic coast. *J. Exp. Mar. Biol. Ecol.* 205:115-135.
- Gittleman, J. L. and P. H. Harvey. 1982. Carnivore home-range size, metabolic needs, and ecology. *Behav. Ecol. Sociobiol.* 10:57-63.
- Gourley, E. V. 1979. Rhythms. *In*: M. Harless and H. Morlock (eds.), *Turtles: Perspectives and Research*. Wiley, New York. pp. 509-520.
- Gregory, L. F. and J. R. Schmid. in review. Stress responses and sex ratio of wild Kemp's ridley sea turtles (*Lepidochelys kempî*) in the northeastern Gulf of Mexico. *Gen. Comp. Endocrinol.*
- Gruber, S. H., D. R. Nelson, and J. F. Morrissey. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. *Bull. Mar. Sci.* 43:61-76.
- Guseman, J. L. and L. M. Ehrhart. 1990. Green turtles on Sabellariid worm reefs: initial results from studies on the Florida Atlantic coast. *In*: T. H. Richardson, J. I. Richardson, and M. Donnelly (comps.), Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278:125-127.
- Hacker, S. D. and R. S. Steneck. 1990. Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71:2269-2285.

- Harris, S., W. J. Creswell, P. G. Forde, W. J. Trehwella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* 20:97-123.
- Heck, K. L., Jr. and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53:125-134.
- Henwood, T. A. and L. H. Ogren. 1987. Distribution and migrations of immature Kemp's ridley turtles (*Lepidochelys kempí*) and green turtles (*Chelonia mydas*) off Florida, Georgia, and South Carolina. *Northeast Gulf Sci.* 9:153-159.
- Hildebrand, H. H. 1963. Hallazgo del area de anidacion de la tortuga marina "lora" *Lepidochelys kempí* (Garman) en la costa occidental del Golfo de Mexico. *Ciencia* 22:105-112.
- Hildebrand, H. H. 1982. A historical review of the status of sea turtle populations in the western Gulf of Mexico. *In*: K. A. Bjorndal (ed.), *Biology and Conservation of Sea Turtles*. Smithsonian Institution Press, Washington, DC. pp. 447-453.
- Hines, A. H. and T. G. Wolcott. 1990. Blue crab movement and feeding measured by ultrasonic telemetry. *Bull. Mar. Sci.* 46:246.
- Humm, H. J. 1973. The biological environment: benthic algae of the eastern Gulf of Mexico. *In*: J. I. Jones, R. E. Ring, M. O. Rinkel, and R. E. Smith (eds.), *A Summary of the Knowledge of the Eastern Gulf of Mexico*. State University System of Florida, Institute of Oceanography, St. Petersburg, FL. pp. IIIB-1 - IIIB-15.
- Ireland, L. C. 1980. Homing behavior of juvenile green turtles, *Chelonia mydas*. *In*: C. J. Amlaner, Jr. and D. W. MacDonald (eds.), *A Handbook on Biotelemetry and Radio Tracking*. Pergamon, Oxford. pp. 761-764.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.

- Kopp, S. D., F. S. Guthery, N. D. Forretser, and W. E. Cohen. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. *J. Wildl. Manage.* 62:884-894.
- Krebs, C. J. 1989. *Ecological Methodology*. HarperCollins, New York. 654 p.
- Lambe, T. W. and R. V. Whitman. 1969. *Soil Mechanics*. Wiley, New York. 553 p.
- Lillywhite, H. B. 1987. Temperature, energetics, and physiological ecology. *In*: R. A. Siegel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York. pp. 422-477.
- Lindberg, W. J. 1980. Behavior of a xanthid crab occupying bryozoan colonies, and patterns of resource use with reference to mating systems. Ph.D. dissertation, Florida State University, Tallahassee, FL. 121 p.
- Lindberg, W. J. and G. Stranton. 1988. Bryozoan-associated decapod crustaceans: community patterns and a case of cleaning symbiosis between a shrimp and a crab. *Bull. Mar. Sci.* 42:411-423.
- Lutcavage, M. and J. A. Musick. 1985. Aspects of the biology of sea turtles in Virginia. *Copeia* 1985:449-456.
- Lutcavage, M. E. and P. L. Lutz. 1997. Diving physiology. *In*: P. L. Lutz and J. A. Musick, *The Biology of Sea Turtles*. CRC Press, Boca Raton, FL. pp. 277-296.
- Lutz, P. L., A. Bergey, and M. Bergey. 1989. Effects of temperature on gas exchange and acid-base balance in the sea turtle *Caretta caretta* at rest and during routine activity. *J. Exp. Biol.* 144:155-169.
- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- Magnuson, J. J., K. A. Bjorndal, W. D. DuPaul, G. L. Graham, D. W. Owens, C. H. Peterson, P. C. H. Pritchard, J. I. Richardson, G. E. Saul, and C. W.

- West. 1990. Decline of the Sea Turtles: Causes and Prevention. National Academy Press, Washington, DC. 274 p.
- Maier, J. A. K. and R. G. White. 1998. Timing and synchrony of activity in caribou. *Can. J. Zool.* 76:1999-2009.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, Chapman & Hall, New York. 177 p.
- Márquez, R. 1994. Synopsis of the Biological Data on the Kemp's Ridley Turtle, *Lepidochelys kempi* (Garman, 1880). NOAA Tech. Memo. NMFS-SEFSC-343, 91 p.
- Márquez, R., R. A. Byles, P. Burchfield, M. Sanchez, J. Diaz, M. A. Carrasco, A. S. Leo, and M. C. Jimenez. 1996. Good news! Rising numbers of Kemp's ridleys nest at Ranch Nuevo, Tamaulipas, Mexico. *Mar. Turtle Newsl.* 73:2-5.
- Márquez, R., J. Díaz, M. Sánchez, P. Burchfield, A. Leo, M. Carrasco, J. Peña, C. Jiménez, and R. Bravo. 1999. Results of the Kemp's ridley nesting beach conservation efforts in México. *Mar. Turtle Newsl.* 85:2-4.
- McClearn, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. *J. Wildl. Manage.* 62:793-801.
- McNab, B. K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.* 97:133-140.
- McNay, R. S., J. A. Morgan, and F. L. Bonnell. 1994. Characterizing independence of observations in movements of Columbian black-tailed deer. *J. Wildl. Manage.* 58:422-429.
- McRae, E. D., Jr. 1950. An ecological study of the xanthid crabs in the Cedar Key area. M.S. thesis, University of Florida, Gainesville, FL. 73 p.

- Mendonça, M. T. 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida Lagoon. *Copeia* 1983:1013-1023.
- Mendonça, M. T. and P. C. H. Pritchard. 1986. Offshore movements of post-nesting Kemp's ridley sea turtles (*Lepidochelys kempî*). *Herpetologica* 42:373-381.
- Menzel, R. W. and F. E. Nichy. 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. *Bull. Mar. Sci. Gulf Caribb.* 8:125-145.
- Meylan, A. 1982. Sea turtle migration - evidence from tag returns. *In*: K. A. Bjorndal (ed.), *Biology and Conservation of Sea Turtles*. Smithsonian Institution Press, Washington, DC. pp. 91-100.
- Miller, D. A., G. A. Hurst, and B. D. Leopold. 1999. Habitat use of eastern wild turkeys in central Mississippi. *J. Wildl. Manage.* 63:210-222.
- Morreale, S. J. and E. A. Standora. 1992. Habitat use and feeding activity of juvenile Kemp's ridleys in inshore waters of the northeastern U.S. *In*: M. Salmon and J. Wyneken (Compilers), *Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-302:75-77.
- Morreale, S. J. and E. A. Standora. 1998. Early life stage ecology of sea turtles in northeastern U.S. waters. NOAA Tech. Memo. NMFS-SEFSC-413. 49 p.
- Morrissey, J. F. 1991. Activity space parameters, home range, diel activity rhythms, and habitat selection of juvenile lemon sharks, *Negaprion brevirostris* (Poey). Ph.D. Dissertation, University of Miami, Coral Gables, FL. 141 p.
- Morse, D. H. 1985. Habitat selection in North American parulid warblers. *In*: M. L. Cody (ed.), *Habitat Selection in Birds*. Academic Press, Orlando, FL. pp. 131-157.

- Musick, J. A. and C. J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. *In*: P. L. Lutz and J. A. Musick, The Biology of Sea Turtles. CRC Press, Boca Raton, FL. pp. 137-163.
- Nieuwolt, P. M. 1996. Movement, activity, and microhabitat selection in the western box turtle, *Ornata luteola*, in New Mexico. *Herpetologica* 52:487-495.
- Nixon, A. J. and S. H. Gruber. 1988. Diel metabolic and activity patterns of the lemon shark (*Negaprion brevirostris*). *J. Exper. Zool.* 248:1-6.
- Nye, L. A. 1990. Telemetric analysis of foraging behavior by blue crabs. *Bull. Mar. Sci.* 46:248.
- Ogden, J. C., L. Robinson, K. Whitlock, H. Daganhardt, and R. Cebula. 1983. Diel foraging patterns in juvenile green turtles (*Chelonia mydas*) in St. Croix United States Virgin Islands. *J. Exp. Mar. Biol. Ecol.* 66:199-205.
- Ogren, L. H. 1989. Distribution of juvenile and subadult Kemp's ridley turtles: preliminary results from the 1984-1987 surveys. *In*: C. W. Caillouet, Jr. and A. M. Landry, Jr. (eds.), Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation, and Management. Texas A & M University Sea Grant College Program, TAMU-SG-89-105:116-123.
- Ormsby, J. P. and R. S. Lunetta. 1987. Whitetail deer food availability maps from Thematic Mapper data. *Photogramm. Engrg. Remote Sens.* 53:1081-1085.
- Orth, R. J. and J. van Montfrans. 1990. Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: a latitudinal perspective. *Bull. Mar. Sci.* 46:126-144.
- Otis, D. L. and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *J. Wildl. Manage.* 63:1039-1044.

- Ott, P. and F. Hovey. 1997. BYCOMP.SAS, Version 1.0.
http://nhsbig.inhs.uiuc.edu/habitat_use/bycomp.sas
- Parrish, J. D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. *Ecology* 76:1813-1820.
- Partridge, L. 1978. Habitat selection. *In*: J. R. Krebs and N. B. Davies (eds.), *Behavioural Ecology: An Evolutionary Approach*. Sinauer Associates, Sunderland, MA. pp. 351-376.
- Pereira, J. M. C. and R. M. Itami. 1991. GIS-based habitat modeling using multiple regression: a study of the Mt. Graham red squirrel. *Photogramm. Engrg. Remote Sens.* 57:1475-1486.
- Porter, W. F. and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. *J. Wildl. Manage.* 51:681-685.
- Powell, E. H., Jr. and G. Gunter. 1968. Observations on the stone crab, *Menippe mercenaria* Say, in the vicinity of Port Aransas, Texas. *Gulf Res. Rep.* 2:285-299.
- Prange, H. D. 1976. Energetics of swimming of a sea turtle. *J. Exper. Biol.* 64:1-12.
- Pritchard, P. C. H. 1969. The survival status of ridley sea turtles in American waters. *Biol. Cons.* 2:13-17.
- Pritchard, P. C. H. and R. Márquez 1973. Kemp's ridley turtle or Atlantic ridley. IUCN Monograph No. 2: Marine Turtle Series. 30 p.
- Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. *Fla. Mar. Res. Pub. No.* 48. 33p.
- Renaud, M. R. 1995. Movements and submergence patterns of Kemp's ridley turtles (*Lepidochelys kempii*). *J. Herpetol.* 29:370-374.

- Renaud, M. R., J. A. Carpenter, J. A. Williams, and S. A. Manzella-Tirpak. 1995. Activities of juvenile green turtles, *Chelonia mydas*, at a jettied pass in south Texas. Fish. Bull. 93:586-593.
- Renaud, M. R. and J. A. Williams. 1997. Movements of Kemp's ridley (*Lepidochelys kempii*) and green (*Chelonia mydas*) sea turtles using Lavaca Bay and Matagorda Bay 1996-1997. Report to Environmental Protection Agency, Office of Planning and Coordination, Region 6, Dallas, TX. 54 p.
- Reynolds, J. E., III, and K. Haddad (Eds.). 1990. Report of the workshop on Geographic Information Systems as an aid to managing habitat for West Indian manatees in Florida and Georgia. Fla. Mar. Res. Pub. No. 49. 57 p.
- Reynolds, T. D. and J. W. Laundré. 1990. Time intervals for estimating pronghorn and coyote home ranges and daily movements. J. Wildl. Manage. 54:316-322.
- Rezak, R., T. J. Bright, and D. W. McGrail. 1985. Reefs and Banks of the Northwestern Gulf of Mexico. Wiley, New York. 259 p.
- Rohmann, S. 1998. NOAA's Medium Resolution Digital Vector Shoreline. <http://www-orca.nos.noaa.gov/projects/shoreline/shoreline.html>
- Ropes, J. W. 1988. The food habits of five crab species at Pettaquamscutt River, Rhode Island. Fish. Bull. 87:197-204.
- Rosenberg, D. K. and K. S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. J. Wildl. Manage. 63:1028-1038.
- Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62:327-335.
- Rosenzweig, M. L. 1985. Some theoretical aspects of habitat selection. In: M. L. Cody (ed.), Habitat Selection in Birds. Academic Press, Orlando, FL. pp. 517-558.

- Rosman, I., G. S. Boland, L. R. Martin, and C. R. Chandler. 1987. Underwater sightings of sea turtles in the northern Gulf of Mexico. U.S. Dept. of the Interior, Minerals and Management Service, OCS Study MMS 87-0107. 37 p.
- Ross, J. P., S. Beavers, D. Mundell, and M. Airth-Kindree. 1989. The Status of Kemp's Ridley. Center for Marine Conservation, Washington, DC. 51 p.
- Rostal, D. C., J. S. Grumbles, R. A. Byles, R. Márquez, and D. W. Owens. 1997. Nesting physiology of Kemp's ridley sea turtles, *Lepidochelys kempfi*, at Rancho Nuevo, Tamaulipas, Mexico, with observations on population estimates. *Chelonian Conserv. and Biol.* 2:538-547.
- Rudloe, A., J. Rudloe, and L. Ogren. 1991. Occurrence of immature Kemp's ridley turtles, *Lepidochelys kempfi*, in coastal waters of northwest Florida. *Northeast Gulf Sci.* 12:49-53.
- SAS Institute Inc. 1989. SAS/STAT User's Guide, Version 6, 4th ed., Vol. 2. SAS, Cary, NC. 846 p.
- Schmid, J. R. 1994. A GIS model for the analysis of marine turtle habitat associations. *In*: K. A. Bjorndal, A. B. Bolten, D. A. Johnson, and P. J. Eliazar (comps.), *Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-351:279-282.
- Schmid, J. R. 1995. Marine turtle populations on the east-central coast of Florida: results of tagging studies at Cape Canaveral, Florida, 1986-1991. *Fish. Bull.* 93:139-151.
- Schmid, J. R. 1998. Marine turtle populations on the west-central coast of Florida: results of tagging studies at the Cedar Keys, Florida, 1986-1995. *Fish. Bull.* 96:589-602.
- Schmid, J. R. and W. J. Barichivich. in prep. Developmental biology and ecology of Kemp's ridley turtles, *Lepidochelys kempfi*, in the eastern Gulf of Mexico. *In*: *Proceedings of a Kemp's Ridley Turtle Symposium Held in Padre Island, March 2, 1999.*

- Schmid, J. R. and L. H. Ogren. 1990. Results of a tagging study at Cedar Key, Florida, with comments on Kemp's ridley distribution in the southeastern U.S. *In*: T. H. Richardson, J. I. Richardson, and M. Donnelly (comps.), Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278:129-130.
- Schmid, J. R. and L. H. Ogren. 1992. Subadult Kemp's ridley sea turtles in the southeastern U.S.: results of long-term tagging studies. *In*: M. Salmon and J. Wyneken (comps.), Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-32:102-103.
- Schmid, J. R. and W. N. Witzell. 1997. Age and growth of wild Kemp's ridley turtles (*Lepidochelys kempi*): cumulative results of tagging studies in Florida. *Chelonian Conserv. and Biol.* 2:532-537.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-141.
- Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *J. Wildl. Manage.* 58:367-374.
- Shaver, D. J. 1991. Feeding ecology of wild and head-started Kemp's ridley turtles in South Texas waters. *J. Herpetol.* 25:327-334.
- Smith, S. A., N. J. Stewart, and J. E. Gates. 1999. Home ranges, habitat selection, and mortality of ring-necked pheasants (*Phasianus colchicus*) in north-central Maryland. *Am. Midl. Nat.* 141:185-197.
- Southeast Area Monitoring and Assessment Program. 1999. South Atlantic Bight Hardbottom Mapping. South Atlantic Bottom Mapping Workgroup. CD-ROM Version 1.1.
- Stabenau, E. K., A. M. Landry, Jr., and C. W. Caillouet, Jr. 1992. Swimming performance of captive-reared Kemp's ridley sea turtles *Lepidochelys kempi* (Garman). *J. Exp. Biol. Ecol.* 161:213-222.

- Standora, E. A., S. J. Morreale, R. Estes, R. Thompson, and M. Hilburger. 1989. Growth rates of juvenile Kemp's ridleys and their movement in New York waters. *In*: S. A. Eckert, K. L. Eckert, and T. H. Richardson (comps.), Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232:175-177.
- Standora, E. A., S. J. Morreale, R. D. Thompson, and V. J. Burke. 1990. Telemetric monitoring of diving behavior and movements of juvenile Kemp's ridleys. *In*: T. H. Richardson, J. I. Richardson, and M. Donnelly (comps.), Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278:133.
- Standora, E. A., S. J. Morreale, and V. J. Burke. 1992. Application of recent advances in satellite transmitter microtechnology: integration with sonic and radio tracking of juvenile Kemp's ridleys from Long Island, NY. *In*: M. Salmon and J. Wyneken (comps.), Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-302:111-113.
- Stasko, A. B. and D. G. Pincock. 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. *J. Fish. Res. Bd. Can.* 34:1261-1285.
- Staus, N. L. 1998. Habitat use and home range of West Indian whistling-ducks. *J. Wildl. Manage.* 62: 171-178.
- Steele, P. and T. M. Bert. 1994. Population ecology of the blue crab, *Callinectes sapidus* Rathbun, in a subtropical estuary: population structure, aspects of reproduction, and habitat partitioning. *Fla. Mar. Res. Publ. No.* 51. 24 p.
- St. Mary, C. M., C. W. Osenberg, T. K. Frazer, and W. J. Lindberg. in press. Stage structure, density dependence, and the efficacy of marine reserves. *Bull. Mar. Sci.*
- Stone, K. D., G. A. Heidt, P. T. Caster, and M. L. Kennedy. 1997. Using geographic information systems to determine home range of the southern flying squirrel (*Glaucomys volans*). *Am. Midl. Nat.* 137:106-111.

- Swihart, R. K. and N. A. Slade. 1985a. Testing for the independence of observations in animal movements. *Ecology* 66:1176-1184.
- Swihart, R. K. and N. A. Slade. 1985b. Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49:1019-1025.
- Swihart, R. K. and N. A. Slade. 1986. The importance of statistical power when testing for independence in animal movements. *Ecology* 67:255-258.
- Szedlmayer, S. T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial reef sites in the northeast Gulf of Mexico. *Copeia* 1997:846-850.
- Timko, R. E. and A. L. Kolz. 1982. Satellite sea turtle tracking. *Mar. Fish. Rev.* 44:19-24.
- Thomas, D. L. and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *J. Wildl. Manage.* 54:322-330.
- Thomas, J. L., R. J. Zimmerman, and T. J. Minello. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bull. Mar. Sci.* 46:115-125.
- Thompson, N., T. Henwood, S. Epperly, R. Lohoefer, G. Gitschlag, L. Ogren, J. Mysing, and M. Renaud. 1990. Marine turtle habitat plan. NOAA Tech. Memo. NMFS-SEFC-255, 20 p.
- Turtle Expert Working Group. 1998. An assessment of the Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) sea turtle populations in the western North Atlantic. NOAA Tech. Memo. NMFS-SEFSC-409. 96 p.
- U. S. Fish and Wildlife Service and National Marine Fisheries Service. 1992. Recovery Plan for the Kemp's Ridley Sea Turtle (*Lepidochelys kempii*). National Marine Fisheries Service, St. Petersburg, FL. 40 p.

- Van Dam, R. P. and C. E. Diez. 1998. Home range of immature hawksbill turtles (*Eretmochelys imbricata* (Linnaeus)) at two Caribbean islands. J. Exp. Mar. Biol. Ecol. 220:15-24.
- Weatherhead, P. J. and D. J. Hoysak. 1988. Spatial and activity patterns of black rat snakes (*Elaphe obsoleta*) from radiotelemetry and recapture data. Can. J. Zool. 67:463-468.
- Wershoven, R. W. and J. L. Wershoven. 1989. Assessment of juvenile green turtles and their habitat in Broward County, Florida waters. In: S. A. Eckert, K. L. Eckert, and T. H. Richardson, (comps.), Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-232:185-187.
- West, N. H., P. J. Butler, and R. M. Bevan. 1992. Pulmonary blood flow at rest and during swimming in the green turtle, *Chelonia mydas*. Physiol. Zool. 287-310.
- White, G. C. and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, New York. 383 p.
- Wiens, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds. In: M. L. Cody (ed.), Habitat Selection in Birds. Academic Press, Orlando, FL. pp. 227-251.
- Wilber, D. H. and W. F. Herrnkind. 1986. The fall emigration of stone crabs *Menippe mercenaria* (Say) from an intertidal oyster habitat and temperature's effect on locomotory activity. J. Exp. Mar. Biol. Ecol. 102:209-221.
- Williams, A. B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC. 550 p.
- Wilson, K. A., K. L. Heck, Jr., and K. W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. Fish. Bull. 85:53-58.

- Wilson, K. A., K. W. Able, and K. L. Heck, Jr. 1990. Habitat use by juvenile blue crabs: a comparison among habitats in southern New Jersey. *Bull. Mar. Sci.* 46:105-114.
- Winter, J. D. 1977. Summer home range movements and habitat use by four largemouth bass in Mary Lake, Minnesota. *Trans. Am. Fish. Soc.* 106:323-330.
- Witzell, W. N. 1998. Long-term tag returns from juvenile Kemp's ridley turtles. *Mar. Turtle Newsl.* 79:20.
- Wolcott, T. G. and A. H. Hines. 1990. Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). *Bull. Mar. Sci.* 46:83-94.
- Wolfe, S. H. (ed.) 1990. An Ecological Characterization of the Florida Springs Coast: Pithlachascotee to Waccasassa Rivers. U. S. Dept. of Interior Biol. Rep. 90(21), December 1990. 323 p.
- Wyneken, J. 1997. Sea turtle locomotion: mechanics, behavior, and energetics. *In*: P. L. Lutz and J. A. Musick, *The Biology of Sea Turtles*, CRC Press, Boca Raton, FL. pp. 165-198.
- Young, T. N., J. R. Eby, H. L. Allen, M. J. Hewitt III, and K. R. Dixon. 1987. Wildlife habitat analysis using landsat and radiotelemetry in a GIS application to spotted owl preference for old growth. *In*: Second Annual International Conference, Exhibits, and Workshops on Geographic Information Systems. San Francisco, CA. pp. 595-600.
- Zug, G. R., H. J. Kalb, and S. J. Luzar. 1997. Age and growth in wild Kemp's ridley sea turtles *Lepidochelys kempii* from skeletochronological data. *Biol. Conserv.* 80:261-268.

APPENDIX A
PERCENT HABITAT COMPOSITIONS FOR COMBINATIONS OF BENTHIC
SUBSTRATES AND INDIVIDUAL BIOLOGICAL ASSEMBLAGES

Primary Substrates

	Habitat types			
	Mud	Sand	Shell	Rock
% study area				
	1.97	81.55	2.16	14.33
% home range				
LK1	0.29	76.55	7.37	15.78
LK2	0.23	76.42	0.00	23.35
LK3	0.15	81.52	2.50	15.83
LK4	0.00	88.65	0.00	11.35
LK5	1.05	79.72	3.25	15.98
LK6	0.05	87.45	0.05	12.45
LK7	0.42	76.00	2.89	20.69
LK8	6.66	74.41	6.14	12.79
LK9	0.34	75.59	3.22	20.85
% locations				
LK1	2.94	79.41	0.00	17.65
LK2	0.00	76.19	0.00	23.81
LK3	0.00	78.05	0.00	21.95
LK4	0.00	83.33	0.00	16.67
LK5	5.56	74.07	0.00	20.37
LK6	0.00	88.89	0.00	11.11
LK7	1.72	79.31	0.00	18.97
LK8	10.34	67.24	1.72	20.69
LK9	3.70	79.63	0.00	16.67

APPENDIX A, continued

Substrates with Rock

	Habitat types						
	Mud	Mud-rock	Sand	Sand-rock	Shell	Shell-rock	Rock
% study area	1.61	0.36	38.33	43.21	1.93	0.23	14.33
% home range							
LK1	0.15	0.15	47.35	29.20	7.23	0.15	15.78
LK2	0.00	0.23	25.57	50.84	0.00	0.00	23.35
LK3	0.08	0.08	38.18	43.34	2.39	0.11	15.83
LK4	0.00	0.00	31.27	57.37	0.00	0.00	11.35
LK5	0.61	0.43	35.94	43.78	2.93	0.33	15.98
LK6	0.00	0.05	42.08	45.41	0.00	0.00	12.46
LK7	0.23	0.19	33.69	42.31	2.52	0.37	20.69
LK8	6.40	0.26	41.64	32.77	6.01	0.13	12.79
LK9	0.00	0.34	31.19	44.41	2.37	0.85	20.85
% locations							
LK1	2.94	0.00	47.06	32.35	0.00	0.00	17.65
LK2	0.00	0.00	23.81	52.38	0.00	0.00	23.81
LK3	0.00	0.00	21.95	56.10	0.00	0.00	21.95
LK4	0.00	0.00	26.19	57.14	0.00	0.00	16.67
LK5	1.85	3.70	40.74	33.33	0.00	0.00	20.37
LK6	0.00	0.00	33.33	55.56	0.00	0.00	11.11
LK7	1.72	0.00	29.31	50.00	0.00	0.00	18.97
LK8	10.34	0.00	27.59	39.66	1.72	0.00	20.69
LK9	0.00	3.70	38.89	40.74	0.00	0.00	16.67

APPENDIX A, continued

Sand with Rock

	Habitat types				
	Mud	Sand	Sand-rock	Shell	Rock
% study area	1.97	38.33	43.21	2.16	14.33
% home range					
LK1	0.29	47.35	29.20	7.37	15.78
LK2	0.23	25.57	50.84	0.00	23.35
LK3	0.15	38.18	43.34	2.50	15.83
LK4	0.00	31.27	57.37	0.00	11.35
LK5	1.05	35.94	43.78	3.25	15.98
LK6	0.05	42.08	45.41	0.00	12.46
LK7	0.42	33.69	42.31	2.89	20.69
LK8	6.66	41.64	32.77	6.14	12.79
LK9	0.34	31.19	44.41	3.22	20.85
% locations					
LK1	2.94	47.06	32.35	0.00	17.65
LK2	0.00	23.81	52.38	0.00	23.81
LK3	0.00	21.95	56.10	0.00	21.95
LK4	0.00	26.19	57.14	0.00	16.67
LK5	5.56	40.74	33.33	0.00	20.37
LK6	0.00	33.33	55.56	0.00	11.11
LK7	1.72	29.31	50.00	0.00	18.97
LK8	10.34	27.59	39.66	1.72	20.69
LK9	3.70	38.89	40.74	0.00	16.67

APPENDIX A, continued

Seagrass

	Habitat types				
	Mud	Sand	Shell	Rock	Seagrass
% study area					
	1.95	63.93	2.12	14.20	17.80
% home range					
LK1	0.29	75.96	7.08	15.78	0.88
LK2	0.23	54.44	0.00	23.12	22.21
LK3	0.15	73.21	2.43	15.79	8.43
LK4	0.00	51.59	0.00	10.96	37.45
LK5	1.05	75.99	3.18	15.94	3.83
LK6	0.00	48.51	0.05	12.24	39.19
LK7	0.42	72.18	2.80	20.60	4.01
LK8	6.66	74.02	5.87	12.79	0.65
LK9	0.34	75.25	3.05	20.85	0.51
% locations					
LK1	2.94	79.41	0.00	17.65	0.00
LK2	0.00	59.52	0.00	23.81	16.67
LK3	0.00	78.05	0.00	21.95	0.00
LK4	0.00	52.38	0.00	16.67	30.95
LK5	5.56	68.52	0.00	20.37	5.56
LK6	0.00	57.14	0.00	11.11	31.75
LK7	1.72	72.41	0.00	18.97	6.90
LK8	10.34	67.24	1.72	20.69	0.00
LK9	3.70	79.63	0.00	16.67	0.00

APPENDIX A, continued

Green Algae

	Habitat types				Green algae
	Mud	Sand	Shell	Rock	
% study area	1.93	58.42	1.97	10.33	27.36
% home range					
LK1	0.29	72.27	6.49	15.49	5.46
LK2	0.15	49.62	0.00	13.86	36.37
LK3	0.15	65.16	2.24	13.13	19.32
LK4	0.00	36.65	0.00	3.19	60.16
LK5	1.01	68.91	2.93	13.77	13.38
LK6	0.05	42.62	0.05	4.71	52.56
LK7	0.33	63.09	2.47	16.73	17.38
LK8	6.66	73.24	5.87	12.79	1.44
LK9	0.34	68.14	2.71	18.98	9.83
% locations					
LK1	2.94	72.06	0.00	17.65	7.35
LK2	0.00	59.52	0.00	16.67	23.81
LK3	0.00	60.98	0.00	12.20	26.83
LK4	0.00	30.95	0.00	4.76	64.29
LK5	5.56	68.52	0.00	16.67	9.26
LK6	0.00	44.44	0.00	1.59	53.97
LK7	1.72	67.24	0.00	17.24	13.79
LK8	10.34	67.24	1.72	20.69	0.00
LK9	3.70	74.07	0.00	16.67	5.56

APPENDIX A, continued

Red Algae

	Habitat types				Red algae
	Mud	Sand	Shell	Rock	
% study area	1.97	77.92	2.09	10.77	7.25
% home range					
LK1	0.29	74.93	6.93	13.27	4.57
LK2	0.23	72.66	0.00	16.62	10.49
LK3	0.15	78.60	2.39	11.84	7.02
LK4	0.00	84.86	0.00	9.56	5.58
LK5	1.05	76.86	3.15	11.86	7.09
LK6	0.05	82.33	0.05	9.63	7.94
LK7	0.42	73.21	2.75	14.91	8.71
LK8	6.66	74.02	5.74	11.88	1.70
LK9	0.34	73.90	2.88	16.61	6.27
% locations					
LK1	2.94	77.94	0.00	14.71	4.41
LK2	0.00	69.05	0.00	19.05	11.90
LK3	0.00	75.61	0.00	17.07	7.32
LK4	0.00	83.33	0.00	11.90	4.76
LK5	5.56	74.07	0.00	18.52	1.85
LK6	0.00	79.37	0.00	6.35	14.29
LK7	1.72	79.31	0.00	13.79	5.17
LK8	10.34	67.24	1.72	20.69	0.00
LK9	3.70	77.78	0.00	9.26	9.26

APPENDIX A, continued

Live Bottom

	Habitat types				Live bottom
	Mud	Sand	Shell	Rock	
% study area	1.97	78.11	1.89	9.01	9.03
% home range					
LK1	0.29	72.57	5.60	9.88	11.65
LK2	0.23	72.59	0.00	13.94	13.25
LK3	0.15	77.87	2.05	9.68	10.25
LK4	0.00	83.47	0.00	6.77	9.76
LK5	1.05	76.25	2.78	9.80	10.12
LK6	0.05	83.66	0.05	7.68	8.56
LK7	0.42	72.88	2.33	12.86	11.51
LK8	6.66	72.32	5.87	8.22	6.92
LK9	0.34	72.03	3.22	13.56	10.85
% locations					
LK1	2.94	77.94	0.00	13.24	5.88
LK2	0.00	73.81	0.00	9.52	16.67
LK3	0.00	73.17	0.00	14.63	12.20
LK4	0.00	80.95	0.00	9.52	9.52
LK5	5.56	70.37	0.00	14.81	9.26
LK6	0.00	80.95	0.00	4.76	14.29
LK7	1.72	75.86	0.00	6.90	15.52
LK8	10.34	67.24	1.72	10.34	10.34
LK9	3.70	74.07	0.00	7.41	14.81

APPENDIX B
PERCENT HABITAT COMPOSITIONS FOR BENTHIC SUBSTRATES AND
PAIRED BIOLOGICAL ASSEMBLAGES

Seagrass-Green Algae

	Habitat types					Green algae
	Mud	Sand	Shell	Rock	Seagrass	
% study area	1.91	51.13	1.93	10.26	17.80	16.97
% home range						
LK1	0.29	71.68	6.19	15.49	0.88	5.46
LK2	0.15	39.82	0.00	13.78	22.21	24.04
LK3	0.15	62.24	2.16	13.09	8.43	13.93
LK4	0.00	21.51	0.00	3.19	37.45	37.85
LK5	1.01	66.81	2.86	13.74	3.83	11.75
LK6	0.00	27.25	0.05	4.66	39.19	28.84
LK7	0.33	60.67	2.38	16.64	4.01	15.98
LK8	6.66	72.85	5.61	12.79	0.65	1.44
LK9	0.34	67.80	2.54	18.98	0.51	9.83
% locations						
LK1	2.94	72.06	0.00	17.65	0.00	7.35
LK2	0.00	47.62	0.00	16.67	16.67	19.05
LK3	0.00	60.98	0.00	12.20	0.00	26.83
LK4	0.00	26.19	0.00	4.76	30.95	38.10
LK5	5.56	64.81	0.00	16.67	5.56	7.41
LK6	0.00	26.98	0.00	1.59	31.75	39.68
LK7	1.72	62.07	0.00	17.24	6.90	12.07
LK8	10.34	67.24	1.72	20.69	0.00	0.00
LK9	3.70	74.07	0.00	16.67	0.00	5.56

APPENDIX B, continued

Seagrass-Red Algae

	Habitat types					Red algae
	Mud	Sand	Shell	Rock	Seagrass	
% study area	1.95	61.50	2.05	10.64	16.61	7.25
% home range						
LK1	0.29	74.34	6.64	13.27	0.88	4.57
LK2	0.23	51.61	0.00	16.39	21.29	10.49
LK3	0.15	70.89	2.31	11.80	7.82	7.02
LK4	0.00	48.61	0.00	9.16	36.65	5.58
LK5	1.05	73.46	3.07	11.82	3.51	7.09
LK6	0.00	46.06	0.05	9.43	36.53	7.94
LK7	0.42	69.57	2.66	14.82	3.82	8.71
LK8	6.66	73.63	5.48	11.88	0.65	1.70
LK9	0.34	73.56	2.71	16.61	0.51	6.27
% locations						
LK1	2.94	77.94	0.00	14.71	0.00	4.41
LK2	0.00	54.76	0.00	19.05	14.29	11.90
LK3	0.00	75.61	0.00	17.07	0.00	7.32
LK4	0.00	52.38	0.00	11.90	30.95	4.76
LK5	5.56	68.52	0.00	18.52	5.56	1.85
LK6	0.00	47.62	0.00	6.35	31.75	14.29
LK7	1.72	72.41	0.00	13.79	6.90	5.17
LK8	10.34	67.24	1.72	20.69	0.00	0.00
LK9	3.70	77.78	0.00	9.26	0.00	9.26

APPENDIX B, continued

Seagrass-Live Bottom

	Habitat types					Live bottom
	Mud	Sand	Shell	Rock	Seagrass	
% study area	1.95	60.98	1.86	8.92	17.26	9.03
% home range						
LK1	0.29	72.12	5.46	9.88	0.59	11.65
LK2	0.23	51.38	0.00	13.78	21.36	13.25
LK3	0.15	69.75	2.01	9.68	8.16	10.25
LK4	0.00	47.21	0.00	6.37	36.65	9.76
LK5	1.05	72.63	2.75	9.80	3.65	10.12
LK6	0.00	45.70	0.05	7.53	38.17	8.56
LK7	0.42	69.11	2.28	12.81	3.87	11.51
LK8	6.66	71.93	5.74	8.22	0.52	6.92
LK9	0.34	71.69	3.05	13.56	0.51	10.85
% locations						
LK1	2.94	77.94	0.00	13.24	0.00	5.88
LK2	0.00	57.14	0.00	9.52	16.67	16.67
LK3	0.00	73.17	0.00	14.63	0.00	12.20
LK4	0.00	50.00	0.00	9.52	30.95	9.52
LK5	5.56	64.81	0.00	14.81	5.56	9.26
LK6	0.00	49.21	0.00	4.76	31.75	14.29
LK7	1.72	68.97	0.00	6.90	6.90	15.52
LK8	10.34	67.24	1.72	10.34	0.00	10.34
LK9	3.70	74.07	0.00	7.41	0.00	14.81

APPENDIX B, continued

Green Algae-Red Algae

	Habitat types				Green algae	Red algae
	Mud	Sand	Shell	Rock		
% study area	1.93	56.62	1.93	7.81	24.47	7.25
% home range						
LK1	0.29	71.24	6.19	13.13	4.57	4.57
LK2	0.15	47.63	0.00	9.26	32.47	10.49
LK3	0.15	63.61	2.16	9.87	17.19	7.02
LK4	0.00	35.66	0.00	2.79	55.98	5.58
LK5	1.01	67.21	2.86	10.38	11.46	7.09
LK6	0.05	40.73	0.05	3.79	47.44	7.94
LK7	0.33	61.14	2.38	11.98	15.47	8.71
LK8	6.66	72.98	5.61	11.88	1.17	1.70
LK9	0.34	67.12	2.54	15.42	8.31	6.27
% locations						
LK1	2.94	72.06	0.00	14.71	5.88	4.41
LK2	0.00	54.76	0.00	11.90	21.43	11.90
LK3	0.00	60.98	0.00	12.20	19.51	7.32
LK4	0.00	30.95	0.00	4.76	59.52	4.76
LK5	5.56	68.52	0.00	14.81	9.26	1.85
LK6	0.00	41.27	0.00	1.59	42.86	14.29
LK7	1.72	67.24	0.00	13.79	12.07	5.17
LK8	10.34	67.24	1.72	20.69	0.00	0.00
LK9	3.70	72.22	0.00	9.26	5.56	9.26

APPENDIX B, continued

Green Algae-Live Bottom

	Habitat types				Green algae	Live bottom
	Mud	Sand	Shell	Rock		
% study area	1.93	56.56	1.74	6.62	24.13	9.03
% home range						
LK1	0.29	68.88	5.01	9.73	4.42	11.65
LK2	0.15	47.78	0.00	8.35	30.47	13.25
LK3	0.15	62.85	1.86	8.24	16.66	10.25
LK4	0.00	35.66	0.00	1.59	52.99	9.76
LK5	1.01	66.49	2.53	8.75	11.10	10.12
LK6	0.05	41.60	0.05	2.77	46.98	8.56
LK7	0.33	60.81	2.00	10.72	14.63	11.51
LK8	6.66	71.15	5.61	8.22	1.44	6.92
LK9	0.34	65.59	2.71	12.71	7.80	10.85
% locations						
LK1	2.94	70.59	0.00	13.24	7.35	5.88
LK2	0.00	57.14	0.00	2.38	23.81	16.67
LK3	0.00	60.98	0.00	7.32	19.51	12.20
LK4	0.00	30.95	0.00	2.38	57.14	9.52
LK5	5.56	66.67	0.00	12.96	5.56	9.26
LK6	0.00	44.44	0.00	1.59	39.68	14.29
LK7	1.72	63.79	0.00	6.90	12.07	15.52
LK8	10.34	67.24	1.72	10.34	0.00	10.34
LK9	3.70	68.52	0.00	7.41	5.56	14.81

APPENDIX B, continued

Red Algae-Live Bottom

	Habitat types					
	Mud	Sand	Shell	Rock	Red algae	Live bottom
% study area	1.97	74.93	1.84	6.68	7.25	7.33
% home range						
LK1	0.29	71.09	5.31	8.11	4.57	10.62
LK2	0.23	69.60	0.00	9.95	10.49	9.72
LK3	0.15	75.37	1.97	7.21	7.02	8.27
LK4	0.00	80.08	0.00	5.38	5.58	8.96
LK5	1.05	73.83	2.71	7.12	7.09	8.21
LK6	0.05	79.00	0.05	5.89	7.94	7.07
LK7	0.42	70.46	2.24	9.13	8.71	9.04
LK8	6.66	71.93	5.61	7.83	1.70	6.27
LK9	0.34	70.51	2.88	10.85	6.27	9.15
% locations						
LK1	2.94	76.47	0.00	11.76	4.41	4.41
LK2	0.00	69.05	0.00	9.52	11.90	9.52
LK3	0.00	70.73	0.00	12.20	7.32	9.76
LK4	0.00	80.95	0.00	4.76	4.76	9.52
LK5	5.56	70.37	0.00	12.96	1.85	9.26
LK6	0.00	74.60	0.00	1.59	14.29	9.52
LK7	1.72	75.86	0.00	5.17	5.17	12.07
LK8	10.34	67.24	1.72	10.34	0.00	10.34
LK9	3.70	74.07	0.00	3.70	9.26	9.26

APPENDIX C
PERCENT HABITAT COMPOSITIONS FOR BENTHIC SUBSTRATES AND
TERTIARY COMBINATIONS OF BIOLOGICAL ASSEMBLAGES AND ALL
ASSEMBLAGES COMBINED

Seagrass-Green Algae-Red Algae

	Habitat types					Green algae	Red algae
	Mud	Sand	Shell	Rock	Seagrass		
% study area	1.91	49.79	1.89	7.75	16.61	14.81	7.25
% home range							
LK1	0.29	70.65	5.90	13.13	0.88	4.57	4.57
LK2	0.15	38.13	0.00	9.19	21.29	20.75	10.49
LK3	0.15	60.87	2.09	9.83	7.82	12.22	7.02
LK4	0.00	20.92	0.00	2.79	36.65	34.06	5.58
LK5	1.01	65.29	2.78	10.34	3.51	9.98	7.09
LK6	0.00	26.38	0.05	3.74	36.53	25.36	7.94
LK7	0.33	58.85	2.28	11.88	3.82	14.12	8.71
LK8	6.66	72.58	5.35	11.88	0.65	1.17	1.70
LK9	0.34	66.78	2.37	15.42	0.51	8.31	6.27
% locations							
LK1	2.94	72.06	0.00	14.71	0.00	5.88	4.41
LK2	0.00	45.24	0.00	11.90	14.29	16.67	11.90
LK3	0.00	60.98	0.00	12.20	0.00	19.51	7.32
LK4	0.00	26.19	0.00	4.76	30.95	33.33	4.76
LK5	5.56	64.81	0.00	14.81	5.56	7.41	1.85
LK6	0.00	23.81	0.00	1.59	31.75	28.57	14.29
LK7	1.72	62.07	0.00	13.79	6.90	10.34	5.17
LK8	10.34	67.24	1.72	20.69	0.00	0.00	0.00
LK9	3.70	72.22	0.00	9.26	0.00	5.56	9.26

APPENDIX C, continued

Seagrass-Green Algae-Live Bottom

	Habitat types					Green algae	Live bottom
	Mud	Sand	Shell	Rock	Seagrass		
% study area	1.91	49.39	1.72	6.60	17.26	14.10	9.03
% home range							
LK1	0.29	68.44	4.87	9.73	0.59	4.42	11.65
LK2	0.15	38.28	0.00	8.35	21.36	18.61	13.25
LK3	0.15	59.96	1.82	8.24	8.16	11.42	10.25
LK4	0.00	20.52	0.00	1.59	36.65	31.47	9.76
LK5	1.01	64.43	2.49	8.75	3.65	9.54	10.12
LK6	0.00	26.43	0.05	2.77	38.17	24.03	8.56
LK7	0.33	58.43	1.96	10.67	3.87	13.23	11.51
LK8	6.66	70.76	5.48	8.22	0.52	1.44	6.92
LK9	0.34	65.25	2.54	12.71	0.51	7.80	10.85
% locations							
LK1	2.94	70.59	0.00	13.24	0.00	7.35	5.88
LK2	0.00	45.24	0.00	2.38	16.67	19.05	16.67
LK3	0.00	60.98	0.00	7.32	0.00	19.51	12.20
LK4	0.00	26.19	0.00	2.38	30.95	30.95	9.52
LK5	5.56	62.96	0.00	12.96	5.56	3.70	9.26
LK6	0.00	26.98	0.00	1.59	31.75	25.40	14.29
LK7	1.72	58.62	0.00	6.90	6.90	10.34	15.52
LK8	10.34	67.24	1.72	10.34	0.00	0.00	10.34
LK9	3.70	68.52	0.00	7.41	0.00	5.56	14.81

APPENDIX C, continued

Seagrass-Red Algae-Live Bottom

	Habitat types					Red algae	Live bottom
	Mud	Sand	Shell	Rock	Seagrass		
% study area	1.95	58.94	1.82	6.60	16.11	7.25	7.33
% home range							
LK1	0.29	70.65	5.16	8.11	0.59	4.57	10.62
LK2	0.23	49.23	0.00	9.80	20.52	10.49	9.72
LK3	0.15	67.82	1.94	7.21	7.59	7.02	8.27
LK4	0.00	44.42	0.00	4.98	36.06	5.58	8.96
LK5	1.05	70.54	2.68	7.12	3.33	7.09	8.21
LK6	0.00	43.60	0.05	5.74	35.60	7.94	7.07
LK7	0.42	66.87	2.19	9.09	3.68	8.71	9.04
LK8	6.66	71.54	5.48	7.83	0.52	1.70	6.27
LK9	0.34	70.17	2.71	10.85	0.51	6.27	9.15
% locations							
LK1	2.94	76.47	0.00	11.76	0.00	4.41	4.41
LK2	0.00	54.76	0.00	9.52	14.29	11.90	9.52
LK3	0.00	70.73	0.00	12.20	0.00	7.32	9.76
LK4	0.00	50.00	0.00	4.76	30.95	4.76	9.52
LK5	5.56	64.81	0.00	12.96	5.56	1.85	9.26
LK6	0.00	42.86	0.00	1.59	31.75	14.29	9.52
LK7	1.72	68.97	0.00	5.17	6.90	5.17	12.07
LK8	10.34	67.24	1.72	10.34	0.00	0.00	10.34
LK9	3.70	74.07	0.00	3.70	0.00	9.26	9.26

APPENDIX C, continued

Green Algae-Red Algae-Live Bottom

	Habitat types						
	Mud	Sand	Shell	Rock	Green algae	Red algae	Live bottom
% study area	1.93	55.07	1.72	5.03	21.68	7.25	7.33
% home range							
LK1	0.29	67.99	4.87	8.11	3.54	4.57	10.62
LK2	0.15	46.48	0.00	5.74	27.41	10.49	9.72
LK3	0.15	61.63	1.82	6.22	14.88	7.02	8.27
LK4	0.00	34.86	0.00	1.39	49.20	5.58	8.96
LK5	1.01	65.11	2.49	6.54	9.54	7.09	8.21
LK6	0.05	39.96	0.05	2.36	42.57	7.94	7.07
LK7	0.33	59.23	1.96	7.74	13.00	8.71	9.04
LK8	6.66	70.89	5.48	7.83	1.17	1.70	6.27
LK9	0.34	64.75	2.54	10.51	6.44	6.27	9.15
% locations							
LK1	2.94	70.59	0.00	11.76	5.88	4.41	4.41
LK2	0.00	54.76	0.00	2.38	21.43	11.90	9.52
LK3	0.00	60.98	0.00	7.32	14.63	7.32	9.76
LK4	0.00	30.95	0.00	2.38	52.38	4.76	9.52
LK5	5.56	66.67	0.00	11.11	5.56	1.85	9.26
LK6	0.00	41.27	0.00	1.59	33.33	14.29	9.52
LK7	1.72	63.79	0.00	5.17	12.07	5.17	12.07
LK8	10.34	67.24	1.72	10.34	0.00	0.00	10.34
LK9	3.70	68.52	0.00	3.70	5.56	9.26	9.26

APPENDIX C, continued

All Biological Assemblages

	Habitat types					Green algae	Red algae	Live bottom
	Mud	Sand	Shell	Rock	Seagrass			
% study area	1.91	48.35	1.70	5.01	16.11	12.36	7.25	7.33
% home range								
LK1	0.29	67.55	4.72	8.11	0.59	3.54	4.57	10.62
LK2	0.15	37.21	0.00	5.74	20.52	16.16	10.49	9.72
LK3	0.15	58.94	1.78	6.22	7.59	10.02	7.02	8.27
LK4	0.00	20.12	0.00	1.39	36.06	27.89	5.58	8.96
LK5	1.01	63.23	2.46	6.54	3.33	8.13	7.09	8.21
LK6	0.00	25.77	0.05	2.36	35.60	21.21	7.94	7.07
LK7	0.33	56.99	1.91	7.69	3.68	11.65	8.71	9.04
LK8	6.66	70.50	5.35	7.83	0.52	1.17	1.70	6.27
LK9	0.34	64.41	2.37	10.51	0.51	6.44	6.27	9.15
% locations								
LK1	2.94	70.59	0.00	11.76	0.00	5.88	4.41	4.41
LK2	0.00	45.24	0.00	2.38	14.29	16.67	11.90	9.52
LK3	0.00	60.98	0.00	7.32	0.00	14.63	7.32	9.76
LK4	0.00	26.19	0.00	2.38	30.95	26.19	4.76	9.52
LK5	5.56	62.96	0.00	11.11	5.56	3.70	1.85	9.26
LK6	0.00	23.81	0.00	1.59	31.75	19.05	14.29	9.52
LK7	1.72	58.62	0.00	5.17	6.90	10.34	5.17	12.07
LK8	10.34	67.24	1.72	10.34	0.00	0.00	0.00	10.34
LK9	3.70	68.52	0.00	3.70	0.00	5.56	9.26	9.26

APPENDIX D
PERCENT HABITAT COMPOSITIONS FOR DEPTH INTERVALS

Depth intervals (Mean Lower Low Water)									
	≤ 0.0 m	0.1 - 0.5 m	0.6 - 1.0 m	1.1 - 1.5 m	1.6 - 2.0 m	2.1 - 2.5 m	2.6 - 3.0 m	> 3.0 m	
% study area	0.17	2.30	8.92	21.72	34.67	23.71	6.77	1.74	
% home range									
LK1	0.15	3.24	7.96	26.55	46.90	14.31	0.88	0.00	
LK2	0.00	0.00	4.13	29.79	44.03	16.92	4.67	0.46	
LK3	0.08	1.48	6.76	22.85	44.90	22.39	1.48	0.08	
LK4	0.00	0.00	0.00	0.40	16.14	42.63	26.69	14.14	
LK5	0.22	2.39	11.39	26.32	39.15	19.41	1.05	0.07	
LK6	0.00	0.00	0.36	9.27	34.58	38.01	13.83	3.94	
LK7	0.05	2.24	12.02	31.03	40.77	13.23	0.61	0.05	
LK8	0.26	5.48	9.66	31.20	48.17	5.09	0.13	0.00	
LK9	0.00	2.03	18.31	43.73	33.56	2.20	0.17	0.00	
% locations									
LK1	0.00	0.00	5.88	38.24	45.59	8.82	1.47	0.00	
LK2	0.00	0.00	4.76	40.48	45.24	4.76	2.38	2.38	
LK3	0.00	0.00	4.88	14.63	56.10	21.95	2.44	0.00	
LK4	0.00	0.00	0.00	0.00	14.29	50.00	16.67	19.05	
LK5	0.00	0.00	12.96	46.30	29.63	9.26	1.85	0.00	
LK6	0.00	0.00	1.59	6.35	19.05	41.27	26.98	4.76	
LK7	0.00	0.00	13.79	41.38	36.21	8.62	0.00	0.00	
LK8	0.00	1.72	1.72	44.83	48.28	3.45	0.00	0.00	
LK9	0.00	0.00	9.26	42.59	42.59	5.56	0.00	0.00	

BIOGRAPHICAL SKETCH

Jeffrey Robert Schmid was born September 25, 1964, in Tallahassee, Florida, to John J. and Susan R. Schmid. He attended elementary through high school in Panama City, Florida, and graduated from Bay High School in June, 1982. In June 1986, he received the degree of bachelor of science in environmental technology and aquaculture from the Florida Institute of Technology, Jensen Beach, Florida. He worked for three years with Mr. Larry H. Ogren at the National Marine Fisheries Service (NMFS) Panama City Laboratory before continuing his formal education. He obtained a master of science in biological sciences from University of South Alabama, Mobile, Alabama, in March 1992. The subject of his research was the morphological and biochemical variation in ladyfish from the northern Gulf of Mexico and southern Caribbean Sea. While completing that degree, he continued to work for NMFS where he conducted a mark-recapture study of marine turtles in the Cedar Keys, Florida. In May 1992, he began his studies toward a doctor of philosophy degree in wildlife ecology and conservation at the University of Florida, Gainesville, Florida. He began working with Mr. Wayne N. Witzell at the NMFS Miami Laboratory during his studies at University of Florida and is presently stationed at the NMFS Miami Laboratory.